

# GULF RESEARCH REPORTS

Volume 3, Number 2

The E. A. Richmond Memorial Number

Ocean Springs, Mississippi

December, 1971

# Gulf Research Reports

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Volume 3 | Issue 2

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January 1971

Edward Avery Richmond (1887-1970)

Gordon Gunter

*Gulf Coast Research Laboratory*

DOI: 10.18785/grr.0302.01

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## Recommended Citation

Gunter, G. 1971. Edward Avery Richmond (1887-1970). *Gulf Research Reports* 3 (2): 156-158.  
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DR. E. A. RICHMOND

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Edward Avery Richmond

1887-1970

Edward Avery Richmond was born June 10, 1887 at Brockton, Massachusetts, and he lived his life in a manner that convinced all who knew him that he was the finest type of New England gentleman. He devoted considerable time during his last 25 years to studying the fauna and flora of Horn Island, which lies off of the Mississippi Gulf Coast. Through Doctor Richmond's work the species of living organisms of Horn Island are better recorded than those of any island on the South Atlantic and Gulf Coasts of the United States.

Avery or Ned Richmond, as he was known to his various associates, had a long and varied professional career as an entomologist and botanist. Between 1913, when he was teaching assistant at Cornell, and 1957, when he retired as foreign plant quarantine inspector of the U. S. Department of Agriculture, he served in the Medical Corps during World War I and the Chemical Warfare Service during World War II; was a county agent at Massachusetts State College; an industrial chemist and an industrial field entomologist and crop protection inspector. Interspersed among these activities were various teaching posts at Dartmouth College, New York University, Columbia University, Simmons College, and Rhode Island State College.

For a good many of his adult years Doctor Richmond's talents were utilized by the U. S. government, first at the Japanese Beetle Laboratory (1924-29), and later as foreign plant quarantine inspector (1945-56). His numerous published works include "Studies on the biology of the aquatic Hydrophilidae" (1920), several articles on the Japanese beetle (1927, 1929, and 1931); "M\*P, a safe and effective spray for insects" (1932); and "Mosquito survey of Horn Island, Mississippi" and miscellaneous newspaper articles.

During the period from February 26, 1944 to February 4, 1945 Doctor Richmond was stationed on Horn Island as health officer with the U. S. Army. It was during this time that he became interested in the wildlife he found existing there and decided to observe and record the animals and plants of the island. Not being sponsored by any organization, the expense and time devoted to his study were his own personal contributions. He was still in the Army during the first year; later, realizing the value of it to the region, I was glad to have Doctor Richmond accept an invitation to live and work at the Gulf Coast Research Laboratory.

Later in connection with this work, facilities at the U. S. National Museum and at the Academy of Natural Sciences at Philadelphia were placed at his disposal. He made good use of



the records of marine fauna of Mississippi which have been maintained in manuscript form since 1950 in a reference collection at the Gulf Coast Research Laboratory.

Doctor Richmond received his B. S. from Dartmouth College in 1912, an M. A. from Cornell University in 1924, and his Ph.D. degree from Massachusetts State College in 1930. In addition to his previously listed teaching posts, he lectured at colleges throughout the east coast.

In the early 1930's he did extensive work in the control of pests in the Cape Cod cranberry bogs and also invented a trap to eliminate Japanese beetles.

Doctor Richmond's second marriage was to Leona Watland Terrell of Washington, D. C., in November of 1952. At the time of his retirement from the U. S. Department of Agriculture, he was stationed at McGuire AFB, N. J., and they made their home in Moorestown, N. J., where they continued to live until his death on July 14, 1970.

His personality found social expression outside the field of science and he was a Mason, a Shriner, and a Rotarian, as well as a deacon in the Congregational Church. He also held memberships in the American Entomological Society, Entomological Society of America, Phi Kappa Psi, Acacia and Sigma Xi.

E. A. Richmond was a dollar-a-year man at this Laboratory for nine years beginning in 1959, and his contributions to the biology of Mississippi were considerable. His papers on that subject are cited herewith:

Richmond, E. A. 1962. The flora and fauna of Horn Island, Mississippi. *Gulf Research Reports* 1(2) : 59-106.

———. 1968. A supplement to the flora and fauna of Horn Island, Mississippi. *Ibid* 2(3) : 213-254.

Gordon Gunter  
Gulf Coast Research Laboratory  
Ocean Springs, Mississippi

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Volume 3 | Issue 2

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January 1971

Notes on Insect Occurrences on the Mississippi Gulf Coast and Offshore Islands

Bryant Mather

DOI: 10.18785/grr.0302.02

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NOTES ON INSECT OCCURRENCES ON THE MISSISSIPPI  
GULF COAST AND OFFSHORE ISLANDS<sup>1</sup>

by

Bryant Mather<sup>2</sup>

213 Mt. Salus Drive, Clinton, Mississippi 39056

Dr. Gordon Gunter (1970) has written that, through the work of Dr. E. A. Richmond, ". . . The species of living organisms of Horn Island are better recorded than those of any large island on the South Atlantic and Gulf Coast." It is to be hoped that Dr. Richmond's work will inspire others to contribute much more to the knowledge of the fauna and flora of the Gulf Coast and its offshore islands. I give here a few notes to place some of Dr. Richmond's work in context, to recognize work by others, and to indicate the paucity of the data.

COLEOPTERA — Cicindelidae

The tiger beetles (Cicindelidae) are among the best known and most widely collected of any group of beetles. Yet R. L. Huber, editor of the quarterly *Cicindela*, wrote me in 1968: "Mississippi is one of the few states that has nothing published on Cicindelidae." Today, the only published lists of Mississippi Cicindelidae are those of Dr. Richmond (1962 p. 86, 1968 p. 234) in which five names are listed: *C. dorsalis sauleyi* (Guer.), *C. trifascia ascendens* (Lec.), *C. hamata lacerata* (Chd.), *C. h. monti* Vaurie, and *M. carolina* L. A recent summary (Mather 1970) indicated that records were available for 22 species from 35 counties of Mississippi. The additional available Gulf Coast records are:

*Cicindela repanda* Dej.: Harrison and Jackson Counties.

*Cicindela punctulata* Oliv.: Hancock and Harrison Counties.

*Cicindela blanda* Dej.: Jackson County.

*Cicindela wapleri* Lec.: All three counties.

*C. dorsalis* and *C. hamata* are known from Deer Island and Ship Island; *C. trifascia ascendens* is known from Ship Island.

NEUROPTERA

As was noted above to be the case with *Cicindelidae*, so far as I am aware, the only published lists of Mississippi Neuroptera are those by Dr. Richmond (1962 p. 79, 1968 p. 231). In these he reported the following:

<sup>1</sup>Contribution No. 199, Bureau of Entomology, Division of Plant Industry, Florida Department of Agriculture and Consumer Services, Gainesville, Florida.

<sup>2</sup>Research Associate, Florida State Collection of Arthropods, Division of Plant Industry, Florida Department of Agriculture and Consumer Services, Gainesville, Florida.

*Symphorobius amicus* (Fitch) : The only other Mississippi record known to me is one female taken by R. and B. Taylor at Handsboro, Harrison County, in October 1966.

*Chrysopa oculata* Say: This is known from Gulfport and Biloxi.

*Brachynemurus longicaudis* (Burm) : The only other Mississippi records of this known to me are of specimens taken by R. and B. Taylor at Biloxi and Handsboro.

*Myrmeleon crudelis* (Walker) : This is also known from Biloxi and Ocean Springs (Taylors) and from Jackson and State College.

*Paranthracis hageni* (Banks) : Dr. Richmond's Horn Island record remains the only one from Mississippi known to me.

*Heoclis americana* (Drury) : The only supplementary Mississippi record that I know of is based on a specimen in the collection at Mississippi State University taken in Lumberton, Lamar County, in 1917 by O. A. Davis.

*Utholodes hageni* (Weele) : Widely taken throughout the state.

## LEPIDOPTERA

The history of the study of Mississippi butterflies has been summarized by Mather and Mather (1958). Two early collectors, Frank Morton Jones and Harold L. O'Byrne, confined their work, in 1910 and 1921 and 1929-1933, respectively, to the Gulf Coast. As far as is known, they did not collect on offshore islands. Neither published his results. Forket (1900) published notes of his observations at Ocean Springs. Skinner (1920) published a report which I quote in full: "Mr. W. C. Dukes of Mobile, Alabama, has recently sent me two specimens of *Synatomidae* from a new locality. They were taken on Cat Island, Mississippi. They are *Cosmosoma auge* Linn. and *Didasys belae* Grote. The former is found in Florida, the West Indies, Central America and South America; the latter, so far as I am aware, has not been recorded outside the State of Florida." This, so far as I know, is all that has ever been published on the Lepidoptera of Cat Island. *Cosmosoma auge*, now known as *C. myrodora* Dyar, is now also known from Ship Island, Horn Island (Richmond 1962), Walthall, Wilkinson, and Covington Counties. *Didasys belae* Grt, is known from Mississippi only from Skinner's 1920 report of its occurrence on Cat Island and from Dr. Richmond's report (1962) of its occurrence on Horn Island.

Robert and Barbara Taylor (1965) summarized the results of their work at Biloxi as it related to the Sphingidae and some other moths. They took specimens representing 24 of the 40

species of sphinx moths then known from Mississippi. They took one male of *Epistor lugubris* (Linn), which is the only record of this species from the Gulf Coast other than that given by Richmond (1962).

Dr. Richmond's 1962 list included *Speyeria cybele cybele* (Fabr), the great spangled fritillary. The significance of this record has been discussed elsewhere (Mather 1966) and is summarized below: Mather and Mather (1958) listed *S. cybele cybele* (Fabr) among the butterflies that were not then known to have been found in but were of probable occurrence in Mississippi. They noted that Lambremont (1954) had reported one male taken at Lafayette, Louisiana, on 2 October 1931, in the collection at Southwestern Louisiana Institute; that H. A. Freeman (1951) had reported it as usually rather scarce in Arkansas; and that Roeber had taken it in southwestern Tennessee. They noted that dos Passos and Grey (1947) had listed it for Tennessee, Illinois, Arkansas, and Oklahoma but not for Mississippi or Louisiana. Through the courtesy of Dr. Gordon Gunter, Director, Gulf Coast Research Laboratory, we were put in touch with Dr. E. A. Richmond whose work on Horn Island (1962) includes a reference to *S. cybele cybele*. Dr. Richmond said (in litt.) that his records indicate that this specimen was taken on 23 September 1944; they do not indicate the determiner of or the disposition of the specimen. Most of the determinations were made at the U. S. National Museum. In January 1962 a search was made in the collections there and it was established that no specimen of *S. cybele* from Mississippi could be found. It was then concluded that while this represented a probable occurrence it could not be regarded as a confirmed record. On 10 June 1963 at Oxford, Lafayette County, Mr. John Daniel took a male of *S. cybele cybele*. Thus *S. cybele cybele* is added to the list of butterflies known to have been taken in Mississippi.

In 1969-1970 there has been a most encouraging increase in the study of the Lepidoptera of the Gulf Coast regions of Mississippi and Louisiana, primarily through the work of Mr. Rick Kergosien of Bay St. Louis and Mr. Gayle Strickland of Baton Rouge. Each of these workers has established the occurrence of a number of species not previously known to exist in the area. Skinner (1920) noted that the two species he recorded for Cat Island were previously known from Florida, and, in one case, only from Florida. Strickland's work has revealed a number of species resident in coastal Louisiana not previously known to occur north of peninsular Florida.

Dr. Richmond and I corresponded between 1961 and 1967. I met him at the Gulf Coast Laboratory in April 1965. When we met he gave me a moth that he had collected on Horn Island the night before. I spread it and sent it to Dr. J. A. Powell of the University of California (Berkeley) who determined it as

*Bactra verutana verutana* Zell; it remains (Richmond 1968, p. 232) the only species of the Family Olethreutidae recorded from Horn Island.

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January 1971

Observations on the Biology of Mudshrimps of the Genus *Callinassa* (Anomura: Thalassinidea) in Mississippi Sound

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*Gulf Coast Research Laboratory*

DOI: 10.18785/grr.0302.03

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## Recommended Citation

Phillips, P. J. 1971. Observations on the Biology of Mudshrimps of the Genus *Callinassa* (Anomura: Thalassinidea) in Mississippi Sound. *Gulf Research Reports* 3 (2): 165-196.

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OBSERVATIONS ON THE BIOLOGY OF MUDSHRIMPS OF  
THE GENUS *CALLIANASSA* (ANOMURA: THALASSINI-  
DEA) IN MISSISSIPPI SOUND<sup>1</sup>

by  
Philip J. Phillips<sup>2</sup>

ABSTRACT

The apparent habitat isolation of the mudshrimps *Callianassa islagrande* Schmitt and *Callianassa jamaicensis louisianensis* Schmitt (Anomura: Thalassinidea) in Mississippi Sound is a function of species-related differences in ability to burrow and survive in the significantly different substrates of each habitat. *C. islagrande* is found only in sand bottomed beaches of the offshore barrier islands, whereas *C. j. louisianensis* is found only in the muddy backwaters of the mainland and Deer Island. Both forms produce deep and extensive permanent or semipermanent burrows in their respective habitat and are probably of some significance in sediment turnover. Laboratory studies show that *C. j. louisianensis* can only burrow efficiently in mud and cannot burrow or survive in sand unless there is sufficient available mud with which this form constructs its burrow walls. The inability of *C. islagrande* to tolerate silt limits its ability to burrow and survive in mud. For this reason *C. islagrande* cannot inhabit the muddy inshore waters. The poor burrowing efficiency of *C. j. louisianensis* in sand is due to a mechanical inability to handle uncohesive sand grains. The foliaceous third maxillipeds and comparatively larger second and third pereopods of *C. islagrande* (compared with those of *C. j. louisianensis*) are adaptations to a sandy habitat, enabling greater burrowing efficiency per unit of effort. Adults and juveniles exhibited the same behavior patterns in aquarium studies. Settling juveniles probably exhibit the same behavior pattern as adults and juveniles.

INTRODUCTION

The purpose of this study was to determine whether substrate type is a factor influencing distribution of the thalassinid crustaceans, *Callianassa jamaicensis louisianensis* Schmitt and *Callianassa islagrande* Schmitt, within Mississippi Sound. These forms produce extensive permanent or semipermanent burrows in the littoral and shallow neritic bottoms. Willis (1942) in a study of the mudshrimps of Grand Isle, Louisiana, found *C. islagrande* only in the clean shifting sand beaches facing the

<sup>1</sup>Modified from a thesis submitted to the faculty of Mississippi State University in partial fulfillment of the requirements for the degree of Master of Science.

<sup>2</sup>Department of Zoology, Mississippi State University, State College, Mississippi, and Gulf Coast Research Laboratory, Ocean Springs, Mississippi.



Gulf of Mexico and *C. jamaicense* only in sheltered, mudbottomed backwaters. A similar situation occurs in Mississippi Sound, wherein *C. islagrande* is found only in the sandy beaches of the offshore barrier islands and *C. j. louisianensis* is found only in the muddy inshore beaches. Other than the original descriptions of these taxa (Schmitt 1935) and the report by Willis (1942), there have been no published studies on these callianassids. An unpublished master's thesis (Friedrichs 1955) for the most part consists of a reiteration of Schmitt's original descriptions, and does not contain any pertinent ecological observations.

#### COLLECTING STATIONS

- |                          |                                      |
|--------------------------|--------------------------------------|
| 1. Ocean Springs (Beach) | 7. Horn Island (West End)            |
| 2. Marsh Point           | 8. Horn Island (near lagoon)         |
| 3. Deer Island           | 9. Horn Island (chimney)             |
| 4. Craveline Bay         | 10. Ship Island (Quarantine Station) |
| 5. Belle Fontaine        | 11. Ship Island (Fort Massachusetts) |
| 6. Biloxi (Beach)        |                                      |

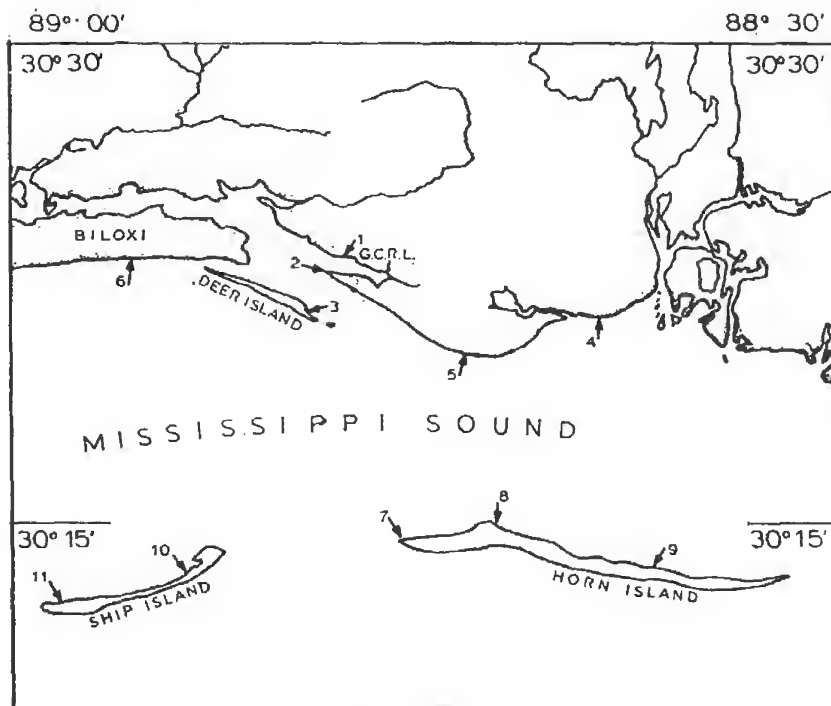


Figure 1  
Mississippi Sound Collecting Stations

*C. j. louisianensis* was collected only at Stations 1 through 6.  
*C. islagrande* was collected only at Stations 7 through 10.

## METHODS AND MATERIALS

### *Collections:*

Collections were made at selected stations in Mississippi Sound (Fig. 1). *C. islagrande* were taken only along the north beaches of Horn and Ship Islands, whereas *C. j. louisianensis* were found only along beaches of the mainland and Deer Island (Table 1, Fig. 1). Initial collections were made using sieve and

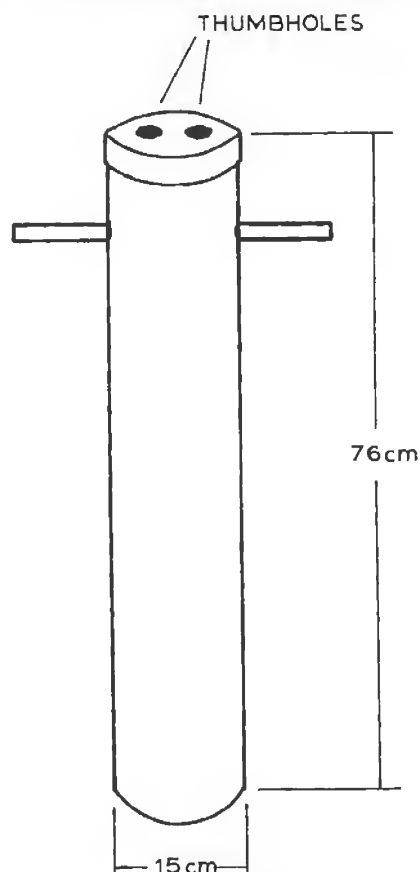


Figure 2

The "Yabby" Pump Used to Collect *C. j. louisianensis*

shovel. Toward the latter part of this study a "yabby" pump (Fig. 2), essentially a hand coring device, was used to collect *C. j. louisianensis*. The use and construction of this pump was described by Hailstone and Stephenson (1961). After the cylinder is pushed into the substrate and extracted with the thumbholes closed, the core is released into a sieve and the mud-

**Table 1:** Collection Data for Callinassid Crustaceans in the Mississippi Sound**A: *C. j. louisianensis***

Locality	Station	Date	Salinity (g/kg)	Tide	No. of Speci- mens	Number of Females	
						w/Ripening Ovarian Eggs	Ovigerous <sup>*</sup>
Ocean Springs Beach	1	1-24-67	4.6	low	4		
	1	2-9-67	12.2	low	2		
	1	2-10-67	12.2	low	3		
	1	2-13-67	11.9	low	7		
	1	2-14-67	12.0	low	3		
	1	3-17-67	16.7	low	5		
	1	3-27-67	20.6	high			
	1	6-19-67	25.0	high	6	1	
Marsh Point	2	2-16-67	10.6	high	8		
	2	2-21-67	14.0	low	3		
	2	2-24-67	12.0	high			
	2	3-3-67	21.6	high	1		
	2	3-8-67	19.0	low	30		
	2	4-3-67	20.8	high	10		
Marsh Point	2	4-17-67	22.8	high	10		
	2	4-24-67	25.0	low	20	1	
	2	4-27-67	24.0	low	17	2	
	2	6-17-67	23.0	low	6	1	
	2	6-22-67	25.0	high	41	6	3 (1 with early ova, 2 with eyespot ova)
Deer Island	3	2-27-67	17.2	high			
	3	3-3-67	24.0	high			
	3	4-11-67	22.3	high	2		
Graveline Bayou	4	3-13-67	15.6	high	3		
Belle Fontaine	5	3-13-67	17.6	high	2		
Biloxi Beach	6	6-13-67	28.0	low	3	1	
<b>B: <i>C. islagrande</i>:</b>							
Horn Island, west end	7	12-2-66	Not measured	low	12		
	7	3-1-67	22.5	high			
	7	3-18-67	24.0	high			
	7	3-22-67	29.4	high	7	2	
Horn Island, near lagoon	8	5-14-67	30.0	high	7		
Horn Island, Chimney	9	4-11-67	27.4	high	4		
	9	4-12-67	27.6	high	3	1	
Ship Island, Quarantine Station	10	3-20-67	30.0	high	15	3	
	10	4-2-67	30.0	low	37	3	
	10	4-22-67	28.2	low	103	9	3 with early ova
Ship Island, Fort Massachusetts	11	3-21-67	27.2	high			

<sup>\*</sup>2 ovigerous females were collected 6-25-51 at Marsh Point; attached ova were at eyespot stage.

shrimps are recovered. The same spot is repeatedly sampled until no more mudshrimps are obtained. This pump is most successfully used on exposed mudflats and considerably less so in sand. The term "yabby" is the Australian common name for *Callinassa australiensis* Dana.

Callianassid collections are best made during periods of low tide with little or no surf action. This combination of factors was seldom encountered. Data for each collection (Table 1) include the following: location, salinity, tide, species, number of specimens and the gross gonadal condition of adult females. Salinity was measured with a sea water hydrometer corrected for temperature.

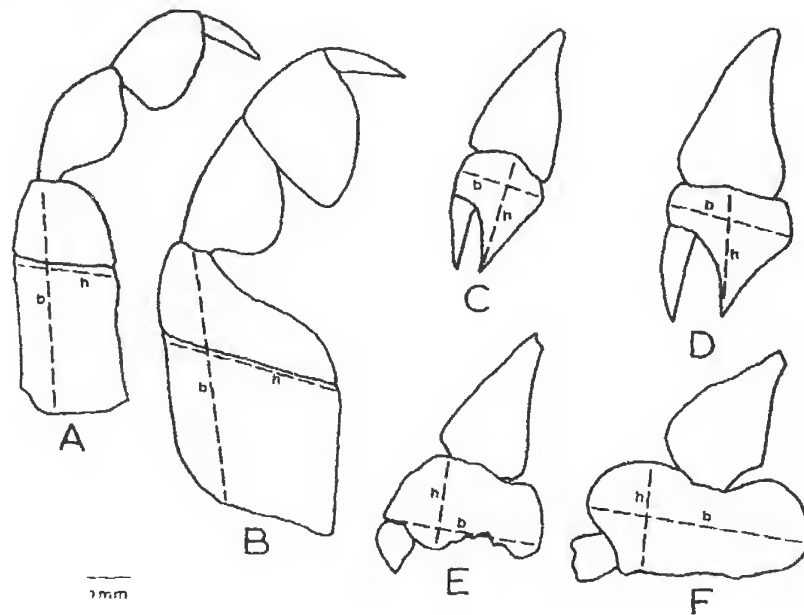


Figure 3

Burrowing Appendages of *C. j. louisianensis* and *C. islagrande*

A: Right third maxilliped of *C. j. louisianensis*.

B: Right third maxilliped of *C. islagrande*.

C: Right second pereopod of *C. j. louisianensis*.

D: Right second pereopod of *C. islagrande*.

E: Right third pereopod of *C. j. louisianensis*.

F: Right third pereopod of *C. islagrande*.

Lines "b" and "h" indicate the length and breadth of the merusischium on the third maxillipeds. Lines "b" and "h" indicate the propodal length and breadth on pereopods.

The two species may be distinguished by differences in the shape of the third maxillipeds (Fig. 3) and uropodal endopodites. In *C. islagrande* the third maxillipeds are foliaceous and the uropodal endopodites are four times as long as broad. *C. j. louisianensis* has periform third maxillipeds and the uropodal endopodites are about one-and-one-half times as long as broad. Sex, in both species, was determined by examination of the first and second pairs of pleopods. The second pair of pleopods of the male are more than twice the length of the first, whereas the first and second pairs of pleopods in the female are of sub-equal length. Ripening ovarian eggs in adult females appear bright yellow to orange through the translucent abdominal exoskeleton. Ovigerous females are those having ova attached to

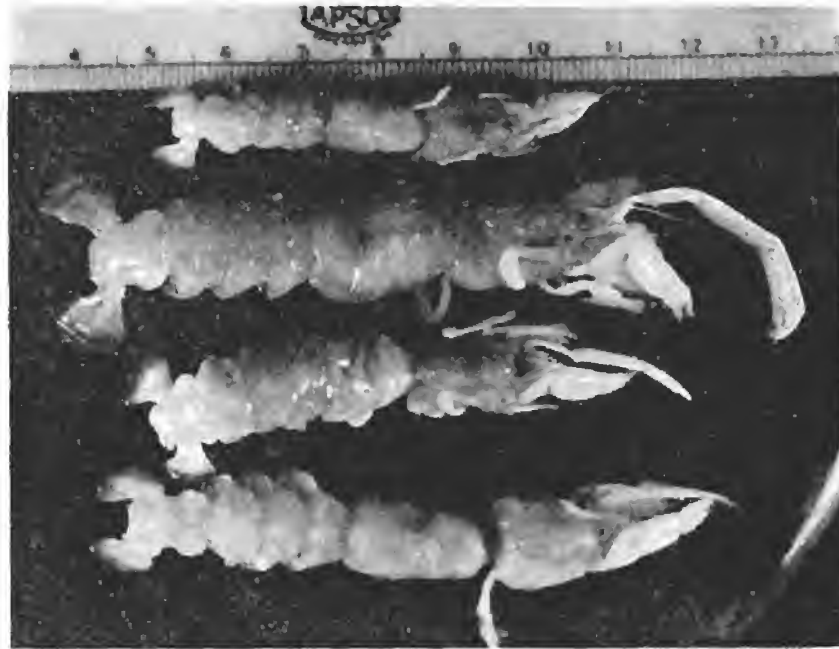


Figure 4

#### Sexual Dimorphism of the Major Cheliped in *C. islagrande*

The top and bottom specimens, females, have major chelipeds less than one-and-one-half times the length of the minor cheliped. The two middle specimens, males, have major chelipeds at least one-and-one-half times the length of the minor cheliped.

the pleopodal setae. During their early development, ova attached to pleopodal setae are bright orange and these recently "berried" females may also have some bright orange ovarian eggs. More advanced ova, in the eyespot stage, have a dull yel-

low color, and females bearing these lack ovarian eggs. Large males of *C. islagrande* have a slender major cheliped which is one-and-one-half times the length of the minor cheliped (Fig. 4). Females of *C. islagrande* have a major cheliped which is less than one-and-one-half times the length of the minor cheliped. There is little sexual dimorphism in cheliped shape of *C. j. louisianensis* and, in both sexes, the major cheliped is less than one-and-one-half times the length of the minor cheliped. Female callianassids may also be recognized by the opening of the oviduct on the coxa of the third pereopod. These openings are larger and more easily distinguished in *C. j. louisianensis* than in *C. islagrande*. Specimens which could not be sexed were classified as juveniles. Mudshrimp were fixed in 20% formalin for 7 days and then transferred to 70% ethanol.

Table 2: Frequency Distribution of Carapace Lengths of Mississippi Sound Callianassids Studied

Carapace Length (mm)	Juveniles		Juveniles		Juveniles	
	<i>C.j.louisianensis</i>	<i>C.islagrande</i>	<i>C.j.louisianensis</i>	<i>C.islagrande</i>	<i>C.j.louisianensis</i>	<i>C.islagrande</i>
2	1					
3	6	1				
4	48	5				
5	40		1		1	
6	12	12	4	3		
7	12	9	6	5	2	1
8		6	3	8	5	2
9		1	4	8	2	4
10		1	6	9	8	9
11		1	5	6	8	11
12			3	8	3	9
13				9		5
14			6	11	1	8
15				11	2	2
16			2	4	4	
17			1	4	3	
18						
19				1		
Totals	99	44	41	87	39	51
Mean Carapace Length (mm)	5.0	5.7	11.8	12.1	12.3	11.3
Variance (sq mm) ( $\pm$ )	2.3	16.1	14.8	11.4	11.7	34.1
Standard Deviation ( $\pm$ )	1.5	4.0	3.8	3.4	3.4	5.8

Carapace lengths and apparent sex ratios of all study material, including specimens from the Gulf Coast Research Laboratory Museum are given in Table 2. Carapace length is

the straight line distance from the tip of the rostrum to the posterior margin of the carapace. All measurements of mudshrimp were made with dividers or calipers and recorded to the nearest one-half mm. Measurements were made of the propodus of the second and third right pereopods and merus and ischium of the right third maxillipeds (Table 3). Certain parameters derived from these data are used in the discussion of the behavior of these callinassids.

**Table 3:** Proportional Measurements (mm) and Surface Area Indices\* of *C. islagrande* and *C. j. louisianensis* in Mississippi Sound

A: <i>C. islagrande</i>									
Carapace Third Maxilliped				Second Pereiopod			Third Pereiopod		
Length	h	b	Index	h	b	Index	h	b	Index
8	3.0	4.5	1.70	2.0	2.0	0.50	2.5	4.0	1.25
8	3.0	4.0	1.66	2.0	2.0	0.50	2.0	4.0	1.00
10	4.0	5.0	2.00	2.5	3.0	0.75	2.0	5.0	1.00
10	4.0	6.5	2.60	3.0	3.0	0.90	3.0	6.0	1.80
11	4.0	6.0	2.09	2.0	2.5	0.45	2.5	5.5	1.25
13	4.0	7.0	2.15	4.0	4.0	1.23	3.0	6.0	1.38
15	6.0	9.0	3.60	3.5	4.0	0.93	3.0	8.0	1.60
15	5.0	8.0	2.66	3.5	4.0	0.93	3.0	8.0	1.60
15	5.0	7.0	2.33	3.5	4.0	0.93	4.0	7.0	1.87
17	6.0	9.0	3.18	4.0	4.0	0.94	4.0	8.0	1.87
Mean indices			2.40	0.81			1.46		

B: <i>C. j. louisianensis</i>									
Carapace Third Maxilliped				Second Pereiopod			Third Pereiopod		
Length	h	b	Index	h	b	Index	h	b	Index
8	1.5	3.5	0.66	2.0	1.0	0.25	1.5	2.5	0.47
8	1.5	3.0	0.56	2.0	1.5	0.38	1.5	2.5	0.47
10	2.0	4.0	0.80	2.5	2.0	0.50	2.0	4.0	0.80
11	2.0	5.0	0.91	2.5	2.0	0.46	2.0	4.0	0.73
12	2.0	5.0	0.83	2.0	1.5	0.25	2.0	4.0	0.66
14	3.0	7.0	1.50	4.0	2.5	0.71	3.0	6.0	1.29
15	3.0	7.5	1.50	4.0	2.5	0.66	2.5	5.0	1.25
15	3.0	8.0	1.60	5.0	3.0	1.00	3.0	7.0	1.40
16	3.0	8.0	1.50	5.0	3.0	0.94	3.0	7.0	1.30
16	3.0	9.0	1.69	4.0	3.0	0.75	3.0	5.5	1.03
Mean Indices			1.12	0.59			0.94		

\*Length (h) x Breadth (b) / Carapace Length = Index of Surface Area (mm) (Fig. 3).

#### Substrate Analysis:

Bottom samples from inshore and offshore collecting sites were analyzed for their relative sand and silt contents by elutriation, the gravimetric fractionation of an unstable suspension

(Priddy *et al.* 1955). Approximately 200 ml samples of fresh bottom material were homogenized for 15 min in a blender and then decanted into 1-liter graduated cylinders. Volumes were adjusted to 1 liter with sea water and the cylinders were shaken vigorously to resuspend the sediments. The samples were allowed to stand for 72 hrs. and then examined to determine the relative proportions of sand and silt by recording the volumetric percentages of the sand and silt layers. The volumetric compositions of bottom samples are given in Table 4.

Table 4: Volumetric Analysis of Selected Mississippi Sound Substrates

Substrate	Occurrence	Percentage Composition by Volume	
		Sand	Silt
Sand	Offshore littoral and neritic zones	98	2
Sand	Inshore littoral zone	80	20
Hard Mud	Inshore littoral and neritic zones	50	50
Clay	Inshore littoral and neritic zones	10	90
Soft Mud	Inshore littoral and neritic zones	traces	100-

#### *Aquarium Studies:*

The objective of these studies was to determine the ability of these mudshrimps to burrow and survive in various substrates from Mississippi Sound and to determine if these calianassids are selective when given a choice of substrates. Aquarium studies of both species were divided into the following categories: (1) tests on individual substrates, (2) tests on stratified substrate columns, (3) tests of superimposing substrate on burrowed specimens and (4) substrate preference tests. Half-liter beakers, graduated cylinders (250 ml, 500 ml, and 1000 ml), shallow pans (26 x 23 x 5 cm and 32 x 26 x 8 cm), mason jars (1 qt), test tubes and 5 and 10 gal tanks served as aquarium vessels. All were aerated by means of an airstone suspended just below the water surface. Except where noted to the contrary, Mississippi Sound water from the habitat of each species was used in these experiments and water depth was never less than 2.5 cm. Specimens were released at the water surface.

In all of the columnar experiments the depth of the upper layer was 8-15 cm and that of the lower was 12-15 cm. In cases where substrate was superimposed on an established mudshrimp colony the depth of the superimposed substrate was 8-9 cm and that of the original substrate layer was about 14 cm. In the substrate preference tests two substrates were placed in apposition in shallow pans. Mudshrimps were released above the interface of the two substrates. The arrangements of substrates in the substrate preference tests are shown in Fig. 5. The sub-



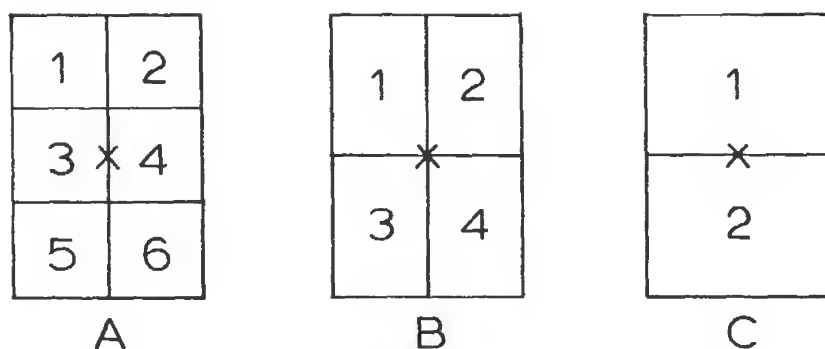


Figure 5

#### Substrate Arrangements in Preference Tests

- A: Test 5. Sectors 1, 4, 5 contain hard mud whereas sectors 2, 3 and 6 contain inshore sand.
- B: Test 6. Sectors 1 and 4 contain hard mud, whereas sectors 2 and 3 contain inshore sand.
- C: Arrangement of All Other Tests: Sector 1 contains one substrate and Sector 2 the other.

In all instances "X" indicates the site at which mudshrimps were released.

strate preference tests, summarized in Table 5, are discussed according to the following categories: (1) sand inshore *versus* sand offshore, (2) sand, either type, *versus* hard mud, (3) sand, either type, *versus* clay and (4) hard mud *versus* clay.

Table 5. Summary of Behavior in Substrate Preference Tests of *Callinassa* of Mississippi Sound

Substrate Combination	Preference	
	<i>C. j. louisianensis</i>	<i>C. islagrande</i>
Sand, inshore <i>versus</i> Sand, offshore	No Preference	Equally Preferred
Sand <i>versus</i> Hard Mud	Hard Mud	Sand
Sand <i>versus</i> Clay	Clay	Sand
Hard Mud <i>versus</i> Clay	Equally Preferred	Hard Mud

Salinity tolerance tests were conducted to determine whether salinity affects the gross behavior of callianassids in the tests involving substrate. The tests (Table 6) show the responses of burrowed and free specimens to the same salinity changes. These experiments were conducted at room temperature (21.1-23.9°C). Salinity tests on free shrimp were conducted by placing the animals in waters of varying salinity. For bur-

rowed shrimp, salinity was adjusted by decanting supernatant water and adding water of the desired salinity.

**Table 6:** Salinity Tolerance Tests on *C. j. louisianensis* and *C. islagrande*

A: Free-swimming Mudshrimps							
Salinity (g/kg)			Species	No. of Specimens	Observations		
From	To	Change			One Hour	Two Days	Five Days
20	20	0	<i>C. j. louisianensis</i>	6	All active	All active	All dead
29	29	0	<i>C. islagrande</i>	6	All active	All active	All dead
20	29	+9	<i>C. j. louisianensis</i>	6	All active	All active	All dead
29	20	-9	<i>C. j. louisianensis</i>	6	All active	All active	All dead
29	20	-9	<i>C. islagrande</i>	6	4 dead	2 torpid	All dead
29	tap water	-29	<i>C. j. louisianensis</i>	7	All active	All active	All dead
29	tap water	-29	<i>C. islagrande</i>	4	All dead		
B: Burrowed Mudshrimps							
20	20	0	<i>C. j. louisianensis</i>	10	All active	All active	All active
29	29	0	<i>C. islagrande</i>	6	All active	All active	All active
20	29	+9	<i>C. j. louisianensis</i>	7	All active	All active	All active
29	20	-9	<i>C. j. louisianensis</i>	6	All active	All active	All active
29	20	-9	<i>C. islagrande</i>	6	All active	All active	All active
20	tap water	-20	<i>C. j. louisianensis</i>	7	All active	All active	All active
29	tap water	-29	<i>C. j. louisianensis</i>	6	All active	All active	All active
29	tap water		<i>C. islagrande</i>	4	Two dead	All dead	

#### *Stomach Content Analyses:*

The stomach contents of recently collected specimens of both taxa and of animals used in the aquarium studies were analyzed. The stomachs were removed and opened. Aliquots of the contents were placed on a slide and examined with a compound microscope fitted with an ocular micrometer. These analyses were performed to determine the nature and size range of particulate stomach contents.

#### FIELD OBSERVATIONS

The bottoms of the inshore Mississippi Sound stations, predominantly muddy, vary from sand to extremely soft mud, whereas those of the offshore stations are uniformly sandy. The compositions of representative bottom samples from the two environments are given in Table 4.

The presence of mudshrimps in a beach can be recognized by their characteristic burrow openings (Fig. 6). There is no apparent species-related difference in the shape or structure



Figure 6

Openings of *C. j. louisianensis* Burrows

Callianassid burrow openings in the natural habitat resemble those produced in the laboratory. This figure shows the surface of Substrate Preference Test 12, 24 hr after the start of the experiment.

Although 10 out of 13 *C. j. louisianensis* were recovered from clay, numerous burrow openings appeared in sand.

of burrow openings. The openings, resembling those reported for other callianasids (Hailstone and Stephenson 1961, Lunz 1937, Pearse *et al.* 1942, Pohl 1946, Weimer and Hoyt 1964), are raised mounds (0.5-2 cm high) with an opening, 0.5-1 cm in diameter, in the center. Openings, often surrounded by fecal pellets, are most abundant in the intertidal bottoms below the belt of surf action and in the shallow neritic zone. On several occasions burrow openings in the inshore and offshore habitats were seen through a maximum water depth of 1.2 m.

The incidence of burrow openings is quite variable in the offshore habitat. At Station 7, the west end of Horn Island (2 December 1966), there was a low tide count of 100+ openings per sq m. During the spring months at the same station there were less than 5 openings per sq m. At Station 9, Ship Island Quarantine Station, during April 1967, there were 100+ open-

ings per sq m. There were no burrow openings at this station on 11 June 1967. No such drastic fluctuations in number of burrow openings were observed in the inshore habitat. It is possible that the fluctuation in number of *C. islagrande* burrow openings results from wind and surf action and does not necessarily represent variations in population density. Certain structural features of the *C. j. louisianensis* burrow wall, discussed later, may also serve to establish a situation wherein the burrow remains long after the mudshrimp has died or otherwise departed. The persistent burrow walls of *C. j. louisianensis* may at times be left protruding as much as 5 cm above the bottom following the displacement of surrounding substrate by strong surf action.

The *in situ* depth of 20 *C. j. louisianensis* burrows, measured by the insertion of flexible plastic tubing, ranged from 32-137 cm (mean, 77 cm). The extreme fragility of burrows of *C. islagrande* prevented similar measurements for that species. Pohl (1946), using this method, found that burrows of *C. major* Say reached a depth of 210 cm.

Burrow walls of both forms vary from 5-15 mm in thickness, but show significant differences in composition. Walls of *C. j. louisianensis* burrows are of very cohesive clay-like mud with a smooth mucilaginous lining, whereas those of *C. islagrande* are composed of loosely cemented sand with no apparent lining. Wall texture of *C. j. louisianensis* burrows is the same, regardless of the composition of the surrounding substrate.

#### BURROWING BEHAVIOR ON SUITABLE SUBSTRATES

Although Willis (1942) reported an ovigerous *C. islagrande* swimming near the water surface, free-swimming mudshrimps were never encountered in this study. Both taxa treated here are certainly capable of at least short term swimming activities. Forward propulsion is achieved by pleopod motions and backward motion is achieved by rapid and repeated flexure of the abdomen. Mudshrimps will swim for a short period, usually for less than 1 min and for a distance of less than 1 m, when first released in an aquarium. They will then invariably cease swimming and burrow headfirst into any acceptable substrate and will be completely hidden within 1 min.

All observations of burrowing behavior and burrow construction were made in the laboratory. Fortunately burrows were frequently constructed against the aquarium wall (Figs. 7 and 8) and direct observation could be made of subsurface activities. In initiating a burrow a mudshrimp usually backs out of the burrow one or more times, depositing displaced substrate near the burrow opening. Excavated material is carried in a basket formed by the third maxillipeds. The burrow ex-

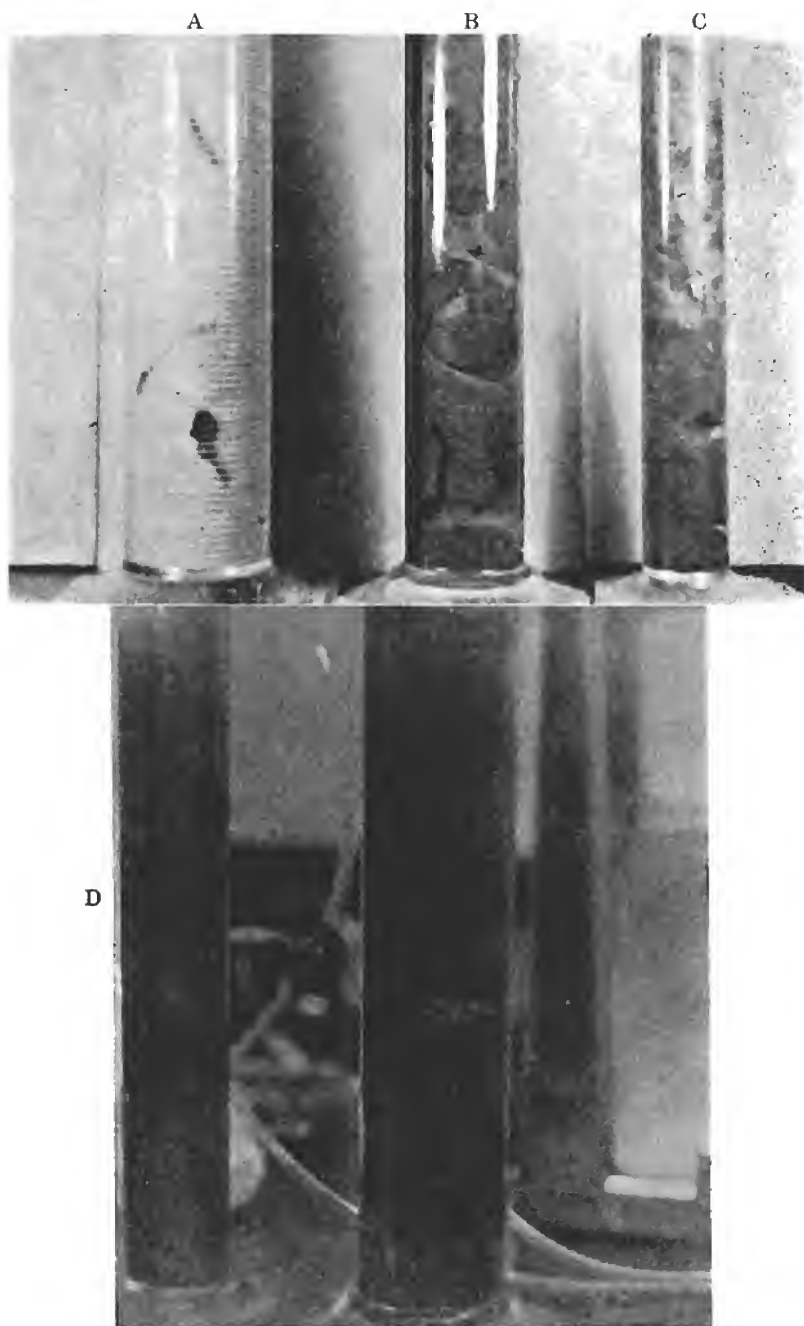


Figure 7

*C. j. louisianensis* and *C. islagrande* Burrows in Suitable Substrates  
 A: Burrows of 2 *C. islagrande* after 2 days in offshore sand.  
 B and C: Burrows of *C. j. louisianensis*, 2 animals in each column, after  
 5 days in mud.  
 D: *C. j. louisianensis* in burrow in habitat substrate.

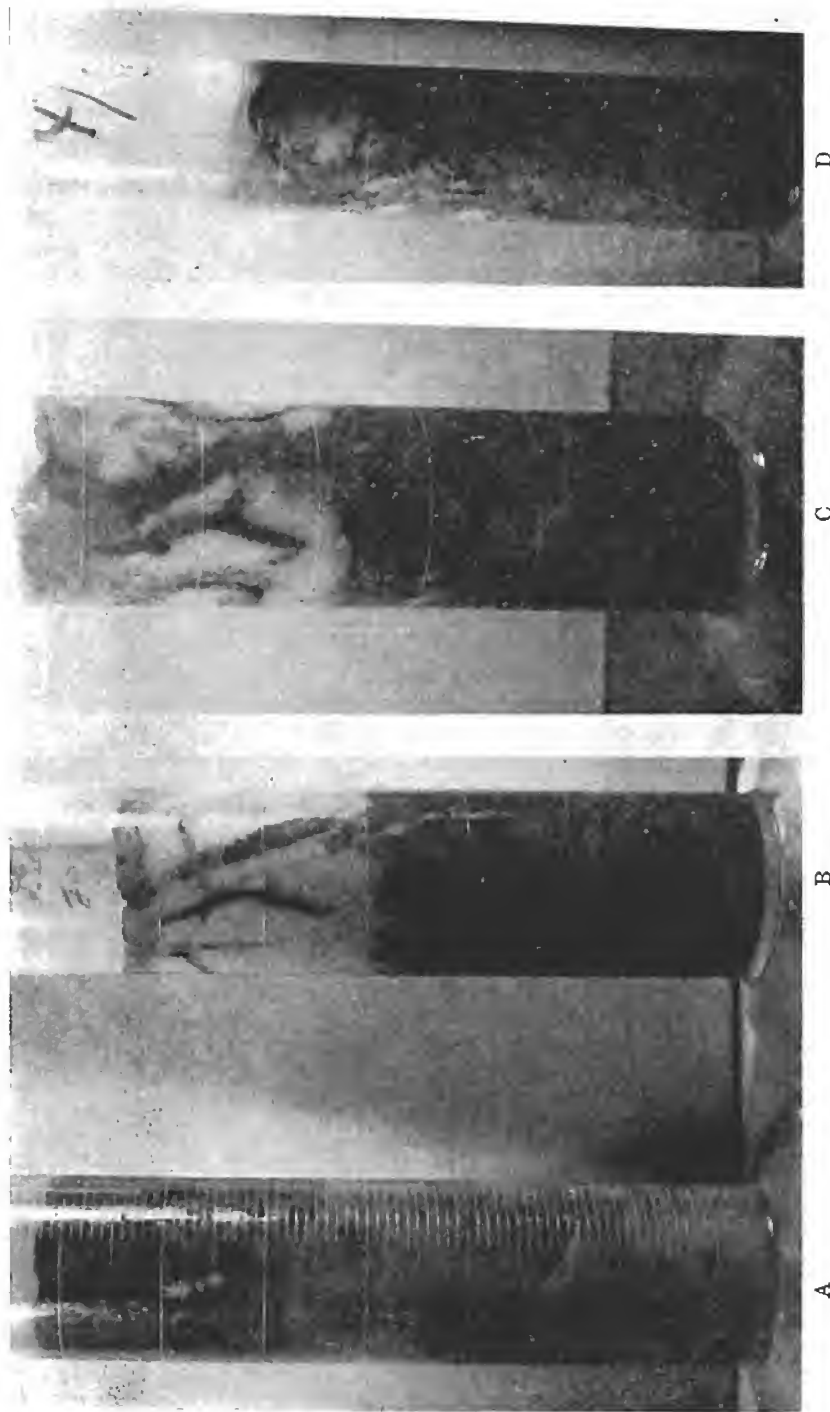


Figure 8 Responses of Burrowed Mudshrimps to Superimposed Substrates. A shows that within 3 days one *C. islagrande* extended its burrow through superimposed mud. B, C and D show progressive thickening of *C. j. louisianensis* mud-lined burrow walls in superimposed sand at 3, 14 and 21 days, respectively. Disturbance of the sand (upper)—mud (lower) interface by the burrowing activities of *C. j. louisianensis* is also evident (B, C, D).

tends downwards vertically or at a slight angle to the vertical axis (a maximum of  $30^\circ$ ). When the burrow is 3-4 times the carapace length of the burrowing animal, an expanded chamber (about twice the diameter of the rest of the burrow) is constructed. This chamber enables the animal to turn around. When these soft bodied animals turn around there is flexure of almost  $180^\circ$  at the junction of the cephalothorax and first abdominal segment. Laboratory observations indicate that mudshrimp only rarely leave the burrows after the construction of the first turning chamber. Additional turning chambers are constructed periodically throughout the burrow. Substrate displaced by further burrowing operations is usually tamped into the burrow walls and, less often, pushed out of the burrow opening.

The complexity of individual burrows increases with time and the aquarium substrate may eventually resemble a maze (Fig. 7). Burrows within aquaria may be deepened at a considerable pace. It was not unusual for both forms, given suitable substrate, to burrow 36 cm, the maximum depth available, within 24 hrs (Fig. 7). This represents a minimum burrow construction rate of the order of 1.5 cm per hr. There is no apparent difference in burrowing rate with respect to size. The diameter of the burrow is usually about twice the breadth of the animal but may vary from 1-5 times this dimension.

Present observations suggest that, under natural conditions, each burrow is occupied by a single callianassid. On one occasion when 20 specimens were held in an aquarium containing 500 ml of substrate, two individuals were seen in the same burrow. The possibility of similarly crowded conditions ever occurring in the natural habitats of local mudshrimp is difficult to conceive.

In both forms, the chelipeds, third maxillipeds and second and third pairs of pereopods are used in burrowing. The chelipeds and third maxillipeds are essential for burrowing. If both chelipeds or both third maxillipeds are missing burrowing does not occur. The chelipeds and third maxillipeds are used to displace substrate in front of the mudshrimp. The third maxillipeds and, to a lesser extent, the second and third pereopods are employed to tamp displaced substrate into the burrow wall. The third maxillipeds are also used to carry substrate from one portion of the burrow to another. The second and third pereopods also function in displacing substrate, but to a considerably lesser extent than the chelipeds. The dactyls of the fourth pair of pereopods are brushlike and are used in cleaning the body surfaces, branchiae and, in the case of ovigerous females, attached ova. The fifth pair of pereopods function in balancing the mudshrimp against the burrow walls.

Callianassids produce a cementing substance used in construction of the burrow wall. Weimer and Hoyt (1964) stated

that *C. major* produces a cementing substance over the entire body surface and that this cementing material is collophonite, an amorphous calcium phosphate. In the case of *C. j. louisianensis* and *C. islagrande*, sand grains and other particulate matter are often embedded in mucoidal strands originating in the vicinity of the third maxillipeds. Possibly secretion of the cementing substance is localized in the vicinity of the third maxillipeds in the taxa included in this study.

Within their burrows, callianassids generate currents which may be involved in respiration with their pleopods (MacGinitie and MacGinitie 1949). Respiratory currents are produced in the branchial chambers by rapid beating of the scaphognaths of the second pair of maxillae and by occasional flushing of the branchial chambers by lateral contraction of the carapace. The epipodites of the first pair of maxillipeds form a shield over the anterior opening of the branchial cavity and possibly function as a barrier to the entry of foreign particles.

#### FEEDING

Feeding behavior appears to be variable in *Callianassa*. Pohl (1946) stated that *C. major* feeds primarily by sifting the substrate for useable organic material, whereas MacGinitie and MacGinitie (1949) considered *Callianassa affinis* Holmes to be a filter feeder. Stomach content analyses of five recently collected specimens of both *C. j. louisianensis* and *C. islagrande* indicate that these taxa feed, at least in part, by sifting through the substrate. In both cases recognizable stomach contents consisted of about 50% sand grains by particle count. Grain diameter ranged from 10-800 $\mu$  and averaged about 107 $\mu$ . The remaining particulate matter consisted of diatoms of the genera *Navicula*, *Pleurosigma*, *Tabellaria*, *Synedra* and *Pinnularia*, bacteria (cocci and bacilli), and significant quantities of shredded brown material which was probably of vegetable origin. Similar stomach contents have been reported for *C. major* (Pohl 1946).

#### COMMENSALS AND PARASITES

About ten percent of the *C. islagrande* collected were infested with the copepod ectoparasite *Clausidium* sp. These were found on all portions of the exoskeleton and not confined to any specific anatomical region. Pohl (*op. cit.*) reported finding a similar parasite of the genus *Clausidium* infesting *C. major* on the Atlantic coast. No ectoparasites were found on *C. j. louisianensis*. Burrows of both Mississippi Sound mudshrimps harbored pinnixid crabs (*Pinnixia cristata* Rathbun), about one to five crabs per burrow. The *Pinnixia* inhabiting *islagrande* burrows exhibited considerable polymorphism with respect to coloration. Those infesting *jamaicense* burrows were uniformly black and were covered with a dense hydroid growth. The significance of the pinnixid polymorphism is unclear, but it is probably related to substrate.



## AQUARIUM STUDIES

### *Responses to Selected Bottom Types:*

#### *a. Sand (inshore and offshore types).*

*C. j. louisianensis* does not burrow readily. Only one specimen of 15 reached the bottom of a 10 cm sand column within 4 days. Remaining specimens constructed only shallow burrows, up to 3 cm deep, and were observed to leave these burrows and swim more or less continuously for periods of up to 8 hours. As much as 15 min. was required to construct a 3 cm burrow, whereas a similar burrow may be constructed within 1 min. in a mud substrate. The single deep burrowing individual survived for 6 weeks, at which time it died of unknown causes outside its burrow. All other specimens exposed to sand died within 5 days. Examination of the burrow wall of the deep burrowing specimen revealed no conspicuous lining. Stomach contents of 10 specimens, five exposed to each sand type (including the sole deep burrowing individual) consisted of a few bacteria only. There was no difference in response to either offshore or inshore sand; both sand types were equally unsuitable.

*C. islagrande* burrows readily in sand of either source. Shallow burrows were usually constructed within 1 minute. Burrows were deep and extensive (Fig. 7). Five specimens were kept in aquaria containing either inshore sand or offshore sand for as long as 2 months, at which time the experiment was terminated. Among five specimens exposed to each sand type, stomach contents consisted of a few bacteria only. Evidently the feeding behavior of *C. islagrande*, in suitable substrates, is altered in the laboratory environment.

#### *b. Hard Mud.*

*C. j. louisianensis* burrow very readily and burrows 3 cm deep are constructed within 1 minute. Burrows in hard mud were deep and very extensive (Fig. 7). The burrow walls were very similar to those in the natural habitat. Mortality over a 2-month period was low, being 3 out of 35 specimens (8.6%). Stomach contents of five specimens kept in aquaria 2 months were very similar to those of recently collected specimens.

*C. islagrande* does not burrow readily in hard mud. Only 22% (4 of 18) burrowed and survived in mud for 5 days. *C. islagrande* which did construct burrows in hard mud did so just as rapidly as in sand. This species evidently has the ability to burrow into mud, although it seldom does so. Death is preceded by blackening of the margins and articulating borders of the exoskeleton and occlusion of the branchial chambers with silt.

c. *Clay*.

*C. j. louisianensis* burrowing behavior was the same as on hard mud.

*C. islagrande* did not survive on clay for more than 5 days. Specimens swam constantly and seldom attempted burrowing. One specimen of the 10 tested constructed a shallow burrow but died in the burrow within 1 hr. As was the case on hard mud, death was preceded by blackening of the exoskeleton and occlusion of the branchial chambers with silt.

d. *Soft Mud*.

*C. j. louisianensis* exhibited the same behavior as on hard mud or clay.

*C. islagrande* exhibited the same behavior on soft mud as on clay with the exception that none of the 15 tested specimens burrowed or attempted to burrow.

Table 7: Burrowing Responses and Survival of *Callianassa* on Selected Mississippi Sound Substrates\*

Substrate	Survival		Construction of Burrows at Least 10 cm Deep	
	<i>C. j. louisianensis</i>	<i>C. islagrande</i>	<i>C. j. louisianensis</i>	<i>C. islagrande</i>
Sand, inshore	Poor	Good	Rare	Frequent
Sand, offshore	Poor	Good	Rare	Frequent
Hard Mud	Good	Poor	Normal	Rare
Soft Mud	Good	Poor	Frequent	Never
Clay	Good	Poor	Frequent	Never

\*A minimum of 15 specimens of each taxon was tested on each substrate.

Behavior in this series of tests is summarized in Table 7 with respect to survival and the relative number that constructed burrows deeper than 3 cm. *C. islagrande* survives well and burrows deeply only in sand, whereas *C. j. louisianensis* shows optimal survival and burrowing activity in mud or clay environments.

*Effects of Columns Composed of Two Substrate Layers on Burrowing Behavior*

a. *Offshore Sand Above Hard Mud*.

*C. j. louisianensis* showed essentially the same behavior pattern in this test as when tested on said previously. Of six specimens, only two had constructed shallow burrows by the second day. After 4 days one of the two specimens that had constructed a shallow burrow reached the lower mud layer and the

five remaining specimens were dead on the sand surface. The mudshrimp reaching the lower mud layer immediately began to line the upper sand burrow with mud. After 2 weeks the entire burrow had a thick mud wall similar to that found in the natural habitat.

*C. islagrande* burrowed readily into the sand, and all four specimens, in two separate trials, reached the bottom of the sand layer within 6 hrs. One burrow was continued into the mud layer 5 days after the start of the experiment, but no additional mud burrows were seen during the 2-week test. All specimens were recovered alive from the sand layer at the termination of the experiment.

b. *Hard Mud Above Offshore Sand.*

*C. j. louisianensis* all burrowed into the mud within 1 min. and reached the bottom of the sand layer within 24 hrs. Within 2 weeks the layering between the sand and mud was sufficiently disturbed by burrowing activities to partially obliterate the previously distinct substrate interface. Burrow walls were similar to those found in the natural habitat.

*C. islagrande* reacted to the hard mud as they did in previous tests. Only one of the four specimens succeeded in burrowing through the mud into the sand layer during a 4-day period. The remaining specimens repeatedly constructed shallow burrows, then left them and spent most of the time swimming. Within 4 days all free specimens were dead. The burrowed individual died within 8 days. In each case the branchial chamber was occluded with silt and the margins and articulating surfaces of the exoskeleton were blackened.

Evidently *C. j. louisianensis* can burrow through sand if there is mud available for burrow wall construction. Availability of sand does not facilitate burrowing or survival of *C. islagrande* in mud.

*Behavior of Colonies to Superimposed Substrate:*

In this series of tests approximately 250 ml of hard mud or offshore sand were superimposed on established colonies of 10 *C. j. louisianensis* in approximately 400 ml of hard mud or 4 *C. islagrande* in the same volume of offshore sand. Depth of the superimposed layer was approximately 8.5 cm and the depth of the base layer was approximately 14 cm.

*C. j. louisianensis* extended their burrows through superimposed mud or sand within 6 hrs. Burrows extending through sand were lined with mud layers which were thickened throughout the course of the test (Fig. 8). Mud linings of the burrows in sand resembled those found in the natural habitat and some disturbance of the sand-mud interface was noted (Fig. 8).

*C. islagrande* burrows were extended through superimposed sand within 6 hours and all four specimens were recovered alive after 4 weeks. One burrow was extended through the superimposed mud layer by the third day (Fig. 8) and all four animals were found dead in the sand layer at the end of 4 days. Portions of the exoskeletons of the dead test animals were blackened and in each case the branchial chambers were occluded by silt. *C. islagrande*, even when established in a suitable substrate, cannot tolerate silt in the environment.

#### *Substrate Preference Tests:*

The results of these tests, detailed in the Appendix, are summarized in Table 6, and discussed according to each category. Observations were made of the numbers of test animals burrowing into each substrate, speed of burrowing (rapid or slow) into each substrate and the number of test animals recovered from each substrate after a minimum period of 24 hrs.

*Category 1: Sand offshore versus sand inshore* (see Appendix Tests 1-4).

*C. j. louisianensis* exhibited the same behavior pattern as when tested on either substrate alone. Both sand types are equally unacceptable and no preference was shown.

*C. islagrande* showed the same response to each sand type. Approximately equal numbers of test animals burrowed into and were recovered from each substrate. Both substrates were equally suitable and burrowing was rapid (within 1 min) in each.

*Category 2: Sand (inshore or offshore) versus hard mud* (see Appendix Tests 5-11).

*C. j. louisianensis* overwhelmingly preferred mud. After one or two attempts to burrow into sand, test animals usually burrowed into mud upon coming into physical contact with it. Numerous burrow openings appeared in sand although most mudshrimps were recovered from the mud.

*C. islagrande* preferred sand. Although a significant number (27%) burrowed rapidly into the hard mud and almost all left their mud burrows within 1 hr and burrowed into the sand upon coming into contact with it. The majority were recovered from the sand. Those specimens recovered from mud had occluded branchial chambers and partially blackened exoskeletons.

*Category 3: Sand (inshore or offshore) versus clay* (see Appendix Tests 12-14).

*C. j. louisianensis* exhibited the same behavior as in Category 2. The muddy substrate was preferred.

*C. islagrande* never initiated burrows in clay. All test animals were recovered from the sand.

*Category 4: Hard mud versus clay* (see Appendix Tests 15, 16).

*C. j. louisianensis* did not favor either substrate. Both clay and mud were equally suitable.

*C. islagrande* did not burrow into clay. Mud was favored, although it was an unsuitable substrate. Behavior on mud approximated that of previous tests, wherein specimens would repeatedly construct shallow burrows, leave them and swim for varying periods of time. Despite the fact that it is a lethal choice, *C. islagrande* favors mud rather than clay when forced to choose between these substrates. The lower silt content of hard mud makes it more acceptable than clay.

These substrate preference tests showed that *C. j. louisianensis* favors the muddy substrate as opposed to sand and did not show any favoritism between clay or mud. *C. islagrande* selected sand as opposed to mud or clay and did not show any favoritism between inshore and offshore sands. When it comes into contact with a substrate in which it can burrow and survive, the callianassid stays there.

#### *Salinity Tolerance Tests:*

On two occasions (substrate preference tests 4, 11 Appendix) 10 out of 25 (40%) and 13 out of 25 (52%) *C. islagrande* died within 1 hr. To determine if this mortality was the result of osmotic shock, salinity tolerance tests were conducted. The results (Table 6) show that free *C. Islagrande* cannot withstand salinity changes from 29 g/kg to 20 g/kg or lower and that the same salinity variations have no apparent effect on *C. j. louisianensis*. As burrowed *C. islagrande* did not show any apparent response to a change from 29 g/kg to 20 g/kg, the substrate probably acts as a buffer against rapid *in situ* salinity changes within the burrow. These tests have shown that, although extreme salinity change may cause mortality in *C. islagrande*, less drastic changes have no apparent effects on the gross behavior of these callianassids.

### DISCUSSION

The habitat isolation, within Mississippi Sound, of *C. j. louisianensis* and *C. islagrande* is apparently a function of species-related differences in ability to burrow and survive in substrates of each habitat. *C. j. louisianensis*, because of poor burrowing efficiency and poor survival in sand is incapable of inhabiting the *C. islagrande* habitat. *C. islagrande*, conversely, as a result of an inability to survive in a silty environment, is incapable of inhabiting the muddy inshore waters. The condition that enables *C. j. louisianensis* to burrow and survive in the

sandy littoral zone of some inshore beaches is the availability of mud with which to construct burrow walls.

Although the mean salinity of the offshore environment is higher than inshore (Christmas *et al.* 1966), both environments are subject to drastic short term salinity fluctuations (Christmas *et al.* 1966, Dawson 1965). The salinity tolerance tests (Table 6) were insufficient to determine whether salinity has any influence on the distribution of these callianassids. Although the salinity records (Table 1) show a lower salinity for the inshore stations than for the offshore stations, there is considerable overlap during the spring months. Drastic salinity change may be responsible for population variations in the natural habitat but apparently has little or no influence on the apparent habitat isolation of these species.

Survival is dependent upon burrowing. MacGinitie (1934) stated that *C. californiensis* Dana soon die if their body surfaces are not in contact with either glass tubing or burrow walls. Pohl (1946) stated that free *C. major* die as a result of starvation. With respect to the forms considered here, starvation is not the cause of death. Both free and burrowed mudshrimps (*C. islagrande* survived 2 months in sand, and the sole *C. j. louisianensis* survived 6 weeks in sand) had stomach contents consisting only of a few bacteria. Evidently feeding is not crucial for short term survival providing the animal can burrow into the substrate. There is at present no adequate explanation for the apparent necessity of burrowing *per se* for survival.

These forms were never observed to leave burrows in suitable substrates during the course of the aquarium studies. Gunter (1945) reported *C. j. louisianensis* from the stomach contents of the sea catfish, *Galeichthys felis* (Linnaeus) and Darnell (1958) reported *Callianassa* sp. from the stomach contents of the blue channel catfish, *Ictalurus furcatus* (Le Sueur). Therefore, callianassids probably leave their burrows on occasion and are subject to predation by these and other bottom feeders.

Although *C. islagrande* has the ability to burrow into hard mud, this form seldom does so and exhibits poor survival in such bottoms even when burrowed. The mortality of *C. islagrande* on muddy substrates is not exclusively a result of an inability to burrow but also of an inability to tolerate silt. The poor survival of *C. j. louisianensis* on sand can only be correlated with an inability to burrow, which is possibly due to a mechanical inability to handle sand, a considerably less cohesive material than mud.

MacGinitie (1934) stated that *C. californiensis* could only live in sand-mud bottoms tenacious enough for the construction of burrow walls. *C. j. louisianensis* evidently requires a more

cohesive substrate than sand. The greater surface areas of both the third maxillipeds and the second and third pereopods in *C. islagrande* (Fig. 3, Table 3) are probably adaptations for living in a sandy bottom. The relatively smaller surface areas of the corresponding appendages of *C. j. louisianensis* limit this form to the effective handling of only muddy substrates. If the product of the length and breadth (b and h, Fig. 3) for the digging surface of each appendage, divided by the carapace length, is taken as an index of surface area, *C. islagrande* has a considerably greater indexed area than *C. j. louisianensis* (Table 3). The merus-ischium surface area of the third maxilliped (Fig. 3) is strikingly different in these species. The pediform third maxilliped of *C. j. louisianensis* has a mean index of 1.12, whereas the foliaceous third maxilliped of *C. islagrande* has a mean index of 2.40. The other two appendages show less striking differences in gross morphology (Fig. 3), but the mean propodal indices of the second and third pereopods are considerably greater in *C. islagrande* (Table 3).

The fact that the sand inhabiting *C. major* also has foliaceous third maxillipeds (Pohl 1946) lends support to the conclusion that a foliaceous third maxilliped is an adaptation to a sandy environment. Since the cementing substance may, in large part, be localized in the vicinity of the third maxillipeds, a greater merus-ischium surface area could also serve to enhance the efficient use of the cementing substance. Greater surface area would likewise be advantageous in feeding, enabling the organism to sift through larger quantities of substrate per unit of effort. This would be especially important in the *C. islagrande* habitat where sand grains account for 98% of the volumetric composition of the substrate (Table 4). Sand grains, however, only account for 50% of the recognizable stomach contents of *C. islagrande*. Evidently this species selectively rejects large quantities of sand. Additional evidence supporting this is shown by the fact that sand grains in the stomach contents were considerably smaller than those of the substrate. Of five specimens examined, the size of ingested sand ranged from 10-800  $\mu$  with a mean of 107 $\mu$ , whereas that of the substrate ranged from 10-1000 $\mu$ , with a mean of about 400 $\mu$ .

The pediform third maxillipeds of *C. j. louisianensis* are apparently inadequate for feeding in sandy bottom. This is supported by the fact that the sole specimen that burrowed and survived 6 weeks in sand had only a few bacteria in its stomach.

There are no gross anatomical differences in the remaining oral appendages of these two forms. This indicates that the major anatomical differences related to feeding activities are the size and shape of the third maxillipeds.

Pearse (1935) noted that there was a habitat isolation of *C. major* and the burrowing thalassinid, *Upogebia affinis* (Say),



at Beaufort, North Carolina. *U. affinis* was found only in muddy bottom and *C. major* was found exclusively in sand. This parallels the situation in the present study. *Upogebia*, however, is not comparable to *C. j. louisianensis* because it is a filter feeder (Pearse 1935, MacGinitie 1930, MacGinitie and MacGinitie 1949) and because adult *Upogebia*, when moved from their burrows, are incapable of constructing new burrows (Pearse 1935, MacGinitie 1930). Pearse (1935) states that *U. affinis* is well adapted for inhabiting a muddy bottom but did not attempt to explain its apparent absence from sand.

From an ecological viewpoint, one group of organisms comparable with callianassids are those polychaetes which feed by the ingestion or sifting of substrates. Both groups are responsible for sediment overturn. MacGinitie (1934) and MacGinitie and MacGinitie (1949) compared *Callianassa* with terrestrial earthworms, stating that both perform the same role in their respective environments. The concept that mud-shrimps are responsible for sediment overturn is supported by the fact that *C. j. louisianensis*, over a relatively short period of time, partially obliterated the originally distinct substrate interface in columnar studies (Fig. 8).

Gordon (1966) demonstrated that the deposit feeding polychaete *Pectinaria gouldii* (Verrill) was responsible for considerable substrate overturn (10 worms per sq m overturning a 6 cm thick surface layer every 15 years). MacGinitie (1934) stated that an average size *C. californiensis* is responsible for complete turnover of 1 sq in. of substrate to a depth of 30 in. in a period of 240 days. There are no quantitative data on the populations of burrowing Mississippi Sound animals and one cannot estimate the relative importance of callianassid populations in the turnover of Mississippi Sound sediments.

Hailstone and Stephenson (1961) reported that *C. australiensis* carry attached ova for 6 weeks, at which time hatching occurs and planktonic larvae invade the bottom within 9 months. The settling larvae resemble small juveniles and have a carapace length of 1-6 mm. In the case of Mississippi Sound callianassids, ovigerous females were taken in the spring and summer months (Table 1). If a similar growth rate can be projected in Mississippi waters, planktonic juveniles apparently enter the substrate during winter and spring months. Most juveniles collected had a carapace length of 4-7 mm (Table 2) and this suggests that entry into the substrate occurred in smaller size classes.

There were no detectable differences in the tested behavior patterns of juveniles and adults. Therefore, settling juveniles are presumed to have the same behavior patterns as the test animals, survival being dependent upon fortuitous contact with a suitable substrate.



## ACKNOWLEDGEMENTS

I would like to express my appreciation to the National Science Foundation for financial support through NSF Research Grant Number GB 3452 to the Gulf Coast Research Laboratory. Acknowledgement is also made to the Gulf Coast Research Laboratory for additional facilities and support.

I would also like to express my appreciation to the people who have aided me in this work. I am especially indebted to Mr. C. E. Dawson and Dr. Walter Abbott for aid in preparation and critical review of the manuscript. I would like to thank Mr. O. D. Ballard for his aid and advice in the preparation of photographs. Many thanks go to Mr. James Franks for his valuable help in collecting callianassids. I would also like to thank Capt. Fred Thompson and Mr. J. Y. Christmas for making many of the field trips possible. I also want to thank the members of my committee for their constructive criticisms. Special thanks go to my wife Carol for her encouragement and patience and to my parents for their unflinching support.

## APPENDIX

### *Results of Substrate Preference Tests*

Except where otherwise noted, substrate arrangement consisted of two equal rectangular sectors (Fig. 5).

*Category 1: Sand, inshore versus sand, offshore*

#### *C. j. louisianensis:*

##### *Test 1:*

Number of Test Animals: 6

Salinity: 10 g/kg

Substrate	No. Burrowing Within 1 hr.	Burrowing Speed	No. Recovered After 24 hrs.
(1) Sand, inshore	3	Slow	2
(2) Sand, offshore	3	Slow	2

Additional Observations: Test animals repeatedly constructed shallow burrows, left them and swam continuously for as long as 8 hrs.

Burrowing time ranged from 10 min. to 1 hr. Two free specimens were found after 24 hrs.

*C. islagrande:*

*Test 2:*

Number of Test Animals: 20

Salinity: 25 g/kg

Substrate	No. Burrowing Within 1 hr.	Burrowing Speed	No. Recovered After 24 hrs.
(1) Sand, inshore	11	Rapid	9
(2) Sand, offshore	9	Rapid	11

*Test 3:*

Number of Test Animals: 20

Salinity: 25 g/kg

Substrate	No. Burrowing Within 1 hr.	Burrowing Speed	No. Recovered After 24 hrs.
(1) Sand, inshore	8	Rapid	10
(2) Sand, offshore	12	Rapid	10

*C. j. louisianensis* and *C. islagrande:*

*Test 4:*

Number of Test Animals: 25 *C. islagrande*

12 *C. j. louisianensis*

Salinity of Test: 20 g/kg

Salinity of *C. islagrande* Colony: 29 g/kg

Substrate	No. Burrowing Within 1 hr.	Burrowing Speed	No. Recovered After 24 hrs.
(1) Sand, inshore	5	Slow	3
	<i>C. j. louisianensis</i>		<i>C. j. louisianensis</i>
	8	Rapid	8
	<i>C. islagrande</i>		<i>C. islagrande</i>
(2) Sand, offshore	7	Slow	3
	<i>C. j. louisianensis</i>		<i>C. j. louisianensis</i>
	7	Rapid	7
	<i>C. islagrande</i>		<i>C. islagrande</i>

Additional Observations: The behavior of *C. j. louisianensis* was similar to that in Test 1. Three free *C. j. louisianensis* were recovered after 24 hrs. Ten free *C. islagrande* died within 1 hr., death apparently due to osmotic shock (Table 6).

*Category 2: Sand (inshore or offshore) versus Hard Mud*  
*C. j. louisianensis:*

*Test 5:*

Number of Test Animals: 4

Salinity: 8 g/kg

Arrangement of Substrates: Six juxtaposed sectors, 3 of mud and 3 of sand (Fig. 5).

Substrate	No. Burrowing Within 1 hr.	Burrowing Speed	No. Recovered After 24 hrs.
(1) Sand, inshore	0		0
(2) Hard Mud	4	Rapid	4
	(2 in sector 4, 1 each in sectors 1 and 5) (Fig. 5A)		(Same number re- covered from sectors of initial burrowing)

*Test 6:*

Number of Test Animals: 4

Salinity: 8 g/kg

Substrate Arrangements: Four juxtaposed sectors, 2 of mud and 2 of sand.

Substrate	No. Burrowing Within 1 hr.	Burrowing Speed	No. Recovered After 24 hrs.
(1) Sand, inshore	0		0
(2) Hard Mud	4	Rapid	4
	(2 in sector 1, 2 in sector 4) (Fig. 5)		(Same number re- covered from sectors of initial burrowing)

*Test 7:*

Number of Test Animals: 7

Salinity: 15 g/kg

Substrate	No. Burrowing Within 1 hr.	Burrowing Speed	No. Recovered After 24 hrs.
(1) Sand, offshore	1	Slow	1
(2) Hard Mud	6	Rapid	6

*C. islagrande:*

*Test 8:*

Number of Test Animals: 12

Salinity: 26 g/kg

Substrate	No. Burrowing Within 1 hr.	Burrowing Speed	No. Recovered After 24 hrs.
(1) Sand, inshore	9	Rapid	6
(2) Hard Mud	3	Rapid	2

Additional Observations: All test animals recovered from mud had occluded branchial chambers and exhibited blackening of the margins and articulating surfaces of the exoskeleton. Four free specimens were dead after 24 hrs., their branchial chambers occluded and exoskeletons blackened.

*Test 9:*

Number of Test Animals: 8

Salinity: 27 g/kg

Substrate	No. Burrowing Within 1 hr.	Burrowing Speed	No. Recovered After 24 hrs.
(1) Sand, inshore	7	Rapid	7
(2) Hard Mud	1	Rapid	1

Additional Observations: All specimens recovered from mud had blackened exoskeletons.

*Test 10:*

Number of Test Animals: 20

Salinity: 27 g/kg

Substrate	No. Burrowing Within 1 hr.	Burrowing Speed	No. Recovered After 24 hrs.
(1) Sand, offshore	14	Rapid	14
(2) Hard Mud	6	Rapid	1

Additional Observations: Five free specimens were found dead, their branchial chambers occluded with silt and margins of the exoskeleton blackened. The specimen recovered from mud exhibited only blackening of the exoskeleton.

*C. j. louisianensis* and *C. islagrande*:

Test 11:

Number of Test Animals: 25 *C. islagrande*  
10 *C. j. louisianensis*

Salinity of Test: 20 g/kg

Salinity of *C. islagrande* Colony: 29 g/kg

Substrate	No. Burrowing Within 1 hr.	Burrowing Speed	No. Recovered After 24 hrs.
(1) Sand, offshore	8 <i>C. islagrande</i>	Rapid	8 <i>C. islagrande</i>
	2 <i>C. j. louisianensis</i>	Slow	1 <i>C. j. louisianensis</i>
(2) Hard Mud	4 <i>C. islagrande</i>	Rapid	4 <i>C. islagrande</i>
	8 <i>C. j. louisianensis</i>	Rapid	8 <i>C. j. louisianensis</i>

Additional Observations: Thirteen free *C. islagrande* died within 1 hr. due to osmotic shock (Table 6). All *C. islagrande* recovered from mud were dead, their branchial cavities occluded with silt and the margins and articulating surfaces of the exoskeleton blackened.

Category 3: Sand, (inshore or offshore) versus Clay

*C. j. louisianensis*:

Test 12:

Number of Test Animals: 13

Salinity: 20 g/kg

Substrate	No. Burrowing Within 1 hr.	Burrowing Speed	No. Recovered After 24 hrs.
(1) Sand, inshore	2	Slow	3
(2) Clay	11	Rapid	10

Additional Observations: Numerous burrow openings appeared in sand and clay sectors (Fig. 6).

Test 13:

Number of Test Animals: 8

Salinity: 20 g/kg

Substrate	No. Burrowing Within 1 hr.	Burrowing Speed	No. Recovered After 24 hrs.
(1) Sand, offshore	0	—	2
(2) Clay	8	Rapid	6

*C. islagrande:*

*Test 14:*

Number of Test Animals: 18

Salinity: 29 g/kg

Substrate	No. Burrowing Within 1 hr.	Burrowing Speed	No. Recovered After 24 hrs.
(1) Sand, offshore	18	Rapid	18
(2) Clay	0	—	0

*Category 4: Hard Mud versus Clay*

*C. j. louisianensis:*

*Test 15:*

Number of Test Animals: 16

Salinity: 15 g/kg

Substrate	No. Burrowing Within 1 hr.	Burrowing Speed	No. Recovered After 24 hrs.
(1) Hard Mud	8	Rapid	8
(2) Clay	8	Rapid	8

*C. islagrande:*

*Test 16:*

Number of Test Animals: 9

Salinity: 29 g/kg

Substrate	No. Burrowing Within 1 hr.	Burrowing Speed	No. Recovered After 24 hrs.
(1) Hard Mud	9	Rapid	8
(2) Clay	0	—	0

Additional Observations: All specimens had their branchial chambers occluded with silt and the margins and articulating surfaces of the exoskeleton blackened.

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# Gulf Research Reports

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Volume 3 | Issue 2

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1971

Survival of the Oyster *Crassostrea virginica* (Gmelin) in the Laboratory Under the Effects of Oil Drilling Fluids Spilled in the Laguna de Tamiahua, Mexico

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DOI: 10.18785/grr.0302.04

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## Recommended Citation

Cabrera, J. 1971. Survival of the Oyster *Crassostrea virginica* (Gmelin) in the Laboratory Under the Effects of Oil Drilling Fluids Spilled in the Laguna de Tamiahua, Mexico. Gulf Research Reports 3 (2): 197-213.  
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SURVIVAL OF THE OYSTER *CRASSOSTREA VIRGINICA*  
(GMELIN) IN THE LABORATORY UNDER THE EFFECTS  
OF OIL DRILLING FLUIDS SPILLED IN THE LAGUNA DE  
TAMIAHUA, MÉXICO

by  
Jorge Cabrera<sup>1</sup>

ABSTRACT

In 1965, 970.12 m<sup>3</sup> of oil drilling fluid were spilled in the Laguna de Tamiahua, Mexico. Laboratory experiments were carried out to determine possible effects of this upon the oyster *Crassostrea virginica*. It was found that drilling fluid reduced the survival of oysters to a significant degree in concentrations above 200 ppm. At turbidities between 200 and 500 ppm, there was 50% survival on the seventh day. *Tanino* in concentrations between 90 and 170 ppm had a drastic effect upon survival which was 50% between the fourth and fifth days. *Bentonita* in 110 to 190 ppm resulted in 50% survival on the eighth day. *Barita* in concentrations between 50 and 65 ppm did not produce noxious effects on the survival of the oysters. Natural mud in concentrations from 200 to 500 ppm was favorable for the survival of oysters.

INTRODUCTION

With the appearance and increase of internal combustion engines, which increased the demand for oil production, the problem of marine pollution became more pronounced (Yee 1967).

This problem occurs in marine waters, coastal lagoons and other aquatic media as well, but when a fisheries resource is involved, the problem acquires importance beyond the purely biological fields. Yee (*op. cit.*) presented selected references on pollution of marine waters as the result of oil drilling and related activities. His work includes articles written since 1950, in many of which the ramifications of this problem are discussed.

Sugimoto *et al.* (1964, 1965) pointed out that on the fishing grounds of the Seto Inland Sea, damage to the fisheries increased with increasing oil pollution.

The mortality of oysters in relation to natural environments and to oil fields has been analyzed by Mackin and Hopkins

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(1962) in Louisiana. Daugherty (1950, 1951) reported experimental results of the effect of some chemicals used in oil well drilling on marine animals, including the oyster (*C. virginica*); this author explains the reason for his work as follows: "With the recent increase of oil wells in Texas bays, the possibility of pollution from chemical compounds used in drilling became important. Exact knowledge of the effect of these compounds on marine organisms was needed."

The magnitude of the problem is in contrast to the amount of information available, as previous works relating to the effect of fluids from oil drilling on animal life, including the oyster, are very few and deal only with adults. Nothing has been published to date concerning the larval stages of oysters, to which the damaging effects of strange elements in the environment could be even more important.

Very little is known of the relationship that may exist between the turbidity produced by muds, normally found around oyster beds in the Laguna de Tamiahua, and herein called natural muds, and the survival of oysters under similar conditions as mentioned also by Mackin and Hopkins (*op. cit.*).

In Mexico we have had occasion to watch several spills, fortunately most of them without drastic biological results, of oil drilling fluids into Tamiahua Lagoon, Veracruz, one of the most important oyster producing localities of Mexico (fig. 1). In this lagoon, 970.12 m<sup>3</sup> of oil drilling fluids were spilled between April and December 1965; this material was composed of 314.79 m<sup>3</sup> of material extracted from the different geological strata and 655.33 m<sup>3</sup> of industrial materials introduced during the drilling (*vide* Villalobos *et al.* 1968, mimeographed).

This investigation was undertaken to clarify the alleged "mortality" and "extermination" of the oyster reefs in Tamiahua Lagoon. The oil company was sued for a considerable sum of money as recompense for the alleged damage. However, the claim has never been proven by any evidence. The Institute of Biology of the National Autonomous University of Mexico was asked to undertake research on this matter and to give an expert opinion. This was included in the work cited (Villalobos *et al.*) along with some of the data in the present article.

The purpose of this article is to report some results of experiments conducted under laboratory conditions to determine the effects of (a) oil drilling fluids used by Pemex in Tamiahua Lagoon; of (b) several compounds used in the drilling fluids; and of (c) natural mud, on the survival of the local oyster.

#### ACKNOWLEDGEMENTS

The author wishes to thank Dr. Alejandro Villalobos-Figueroa, leader of the project, whose direction and support were

the principal factors in the progress of the project; and Dr. Gordon Gunter, Director of the Gulf Coast Research Laboratory, Ocean Springs, Mississippi, USA, who kindly joined us in camp at Cucharas and in the Laboratory in Mexico City during September 1967 and whose advice and constructive recommendations were appreciated. It must be noted that Doctor Gunter feels that the experiment reported here should be repeated until the results are more satisfactorily proven. The author is in agreement, but considering the lack of economic resources needed, wished to make these incomplete results available to persons interested in this matter. Dr. Sammy M. Ray was kind enough to provide us with copies of the articles of F. M. Daugherty cited herein, and with other interesting information as well.

Many of my co-workers and friends helped in the construction of aquaria in Cucharas, and also in many other ways; special thanks are hereby expressed to the following: Guadalupe de la Lanza, Fernando Manrique, Samuel Gómez, Andrés Reséndez, Virgilio Arenas, Alberto Ramírez, Gerardo Green and Luis Soto.

Many of the residents of Cucharas and La Laja, Veracruz, were of great help in the every day course of our experimental work, for which I am also very grateful. Drs. A. Villalobos and G. Gunter reviewed and criticized this article. Dr. Allan Phillips assisted in the preparation of the English version.

I also wish to thank: ingenieros Graciano Bello, Guillermo Bernal, Enrique Noguera, Ignacio Cervantes and their collaborators, for their extensive assistance in the field work. The experimental work was made possible by the economic support of Petroleos Mexicanos (PEMEX), under contract to the Instituto de Biología, Universidad Nacional Autónoma de México.

## MATERIAL AND METHODS

The oysters used in the experiments came from the Laguna de Tamiahua, particularly from the oyster reefs known as follows: Restinga de Cucharas, La Martinica and Boqueron de Burros (fig. 1). These organisms belong taxonomically to *Crassostrea virginica* (Gmelin), and their medium size was 8 cm in length, with a range from 7 to 12 cm. These oysters were collected with "gafas," an instrument composed of two wooden rakes, 3 meters long, joined a third of the way up, the teeth being nails set in two lines, one opposite the other. These instruments are modified oyster tongs made of wood and nails. Oysters were kept under laboratory conditions for 3 to 5 days before being used in the experiments.

A working place was improvised in the Pemex camp, in the village of Cucharas (fig. 1). A system with a capacity to supply

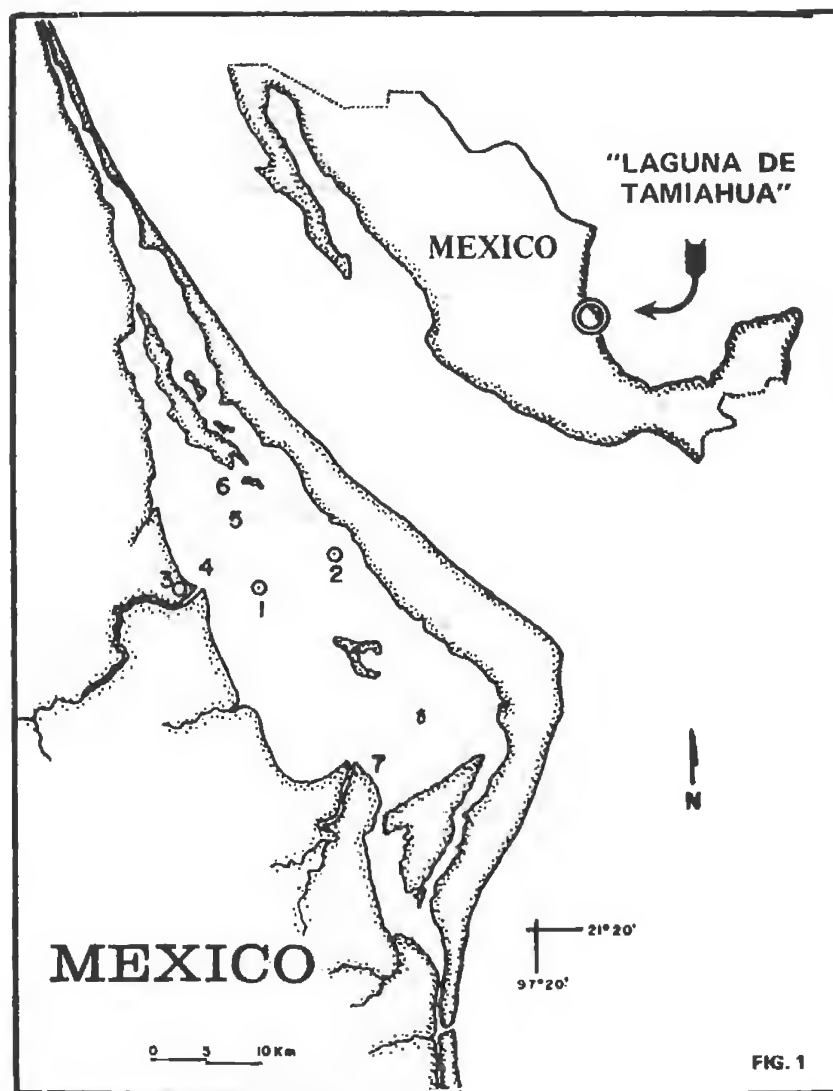


Fig. 1. *Laguna de Tamiahua*:

- 1) Catán oil well
- 2) Acamaya oil well
- 3) Village and estuary of *Cucharas*
- 4) *Restinga de Cucharas* (oyster reef)
- 5) *Restinga la Martinica* (oyster reef)
- 6) *Boquerón de Burros* (oyster reef)
- 7) *Campanario* (mud test site)

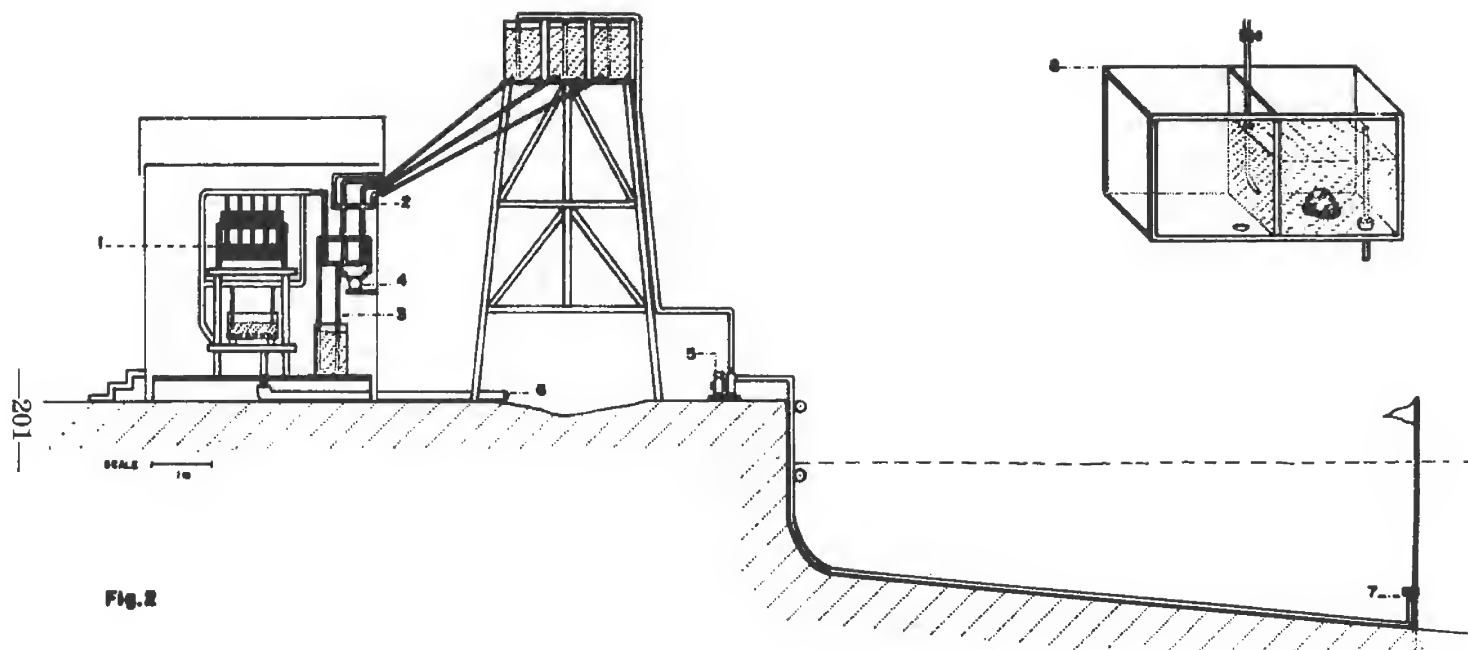


Fig. 2. Diagram of the system used to supply water and suspended material to the aquaria:

- |  |   |
|--|---|
| 1) Aquaria                                   | 5) Pump to raise water to the upper tanks |
| 2) Plastic tubing                            | 6) Outlet                                 |
| 3) Suction tube for suspended material       | 7) Intake                                 |
| 4) Plastic pump to inject suspended material | 8) Aquaria with one oyster each           |

80 aquaria, each containing 8 liters, was built (fig. 2). Proportions of the aquaria were 20 x 20 x 20 cm, in units of two, back-to-back (fig. 2). Each one had a glass excess drainage tube to regulate the water level. Wooden tables covered with water-proof resin were made as well as supports for the aquaria. The whole system was installed in a wooden cottage.

The water used in the experiments came from the Estero de Cucharas (fig. 1), at a point where a little pier extended some 10 meters from the shore in front of the encampment. It was taken at 40 to 60 cm above the bottom in water of 2 or 2.5 meters deep (fig. 2). The water was raised by "Sentinel" pump, model C 1½ A, powered by a Briggs and Stratton 4-cycle gasoline engine. The water was stored in three asbestos-cement tanks having total capacity of 600 liters. These tanks were located on top of a metal tower 5 meters high.

Water was then distributed by gravity, using a system of plastic and P.V.C. tubing and valves, to adjust the water flow in each aquarium. Water was changed simultaneously in all the aquaria three times a day, each change taking 15 minutes at a flow of two liters per minute; this was done at intervals of approximately eight hours. At the time of changing the water, either test fluids or muds were added to the system by means of a plastic pump (Desmo Plastic-Tec, S. A.) driven by a ¼ H. P. electric motor (Power Electrica S. A.) There was some difficulty in running electric motors in Cucharas, as (at the time of this work) the village lacked public power, so a small diesel electric plant was used according to our needs.

Ingenieros Melesio Muñoz R. and Héctor Soto Rosiles, of the Drilling Department of Pemex, provided the drilling fluids needed for the experiments. They also provided information on the chemical compositions of the drilling fluids, which we were not in a position to analyze. According to this information, the drilling fluid was composed of two fractions: one a combination of different commercial substances and the other the various materials extracted from the geologic strata. The fluid used in the experiments came from a drilling located close to the Laguna de Tamiahua, and made at the same time that the oyster survival experiments were run.

The two above-mentioned engineers were of the opinion that the geologic structure of this drilling was quite similar to that found in the Laguna de Tamiahua; that there were no important differences in the drilling procedures; and that the drilling fluids used in the oyster survival experiments were very similar quantitatively and qualitatively to these spilled in the Laguna de Tamiahua.

The following list of materials introduced in the drilling in the Laguna de Tamiahua, and in what proportions, was pro-

vided by the personnel of Pemex (the names of the chemicals are those known in Mexico, with their sources).

	Kg.	%
Barita ..... (Industria Mexicana, S. A., Av. Madero 16, despacho 305, México, D. F.)	6000	6.5
Bentonita ..... (Industria Mexicana, S. A.)	20300	22.0
Pirofosfato tetrasódico ..... (Hooker Mexicana, S. A., Apartado Postal 7529, México 1, D. F.)	1330	1.4
Tanino Cabel ..... (Productos Cabel, S. A., Génova 39-105, Mexico 6, D. F.)	815	0.8
Tinex ..... (Oleoquímica Monterrey, S. A., Montana 13, 7º Piso, México 18, D. F.)	200	0.2
C.M.C. .... (Deribados Macroquímicos, S. A., Durango 283, México, D. F.)	240	0.2
Obturante #8 ..... (Productora y Abastecedora, S. A., Apartado Postal 19-512, México, D. F.)	350	0.3
Lubrisesa ..... (Sosa Escamas, S. A., Apartado Postal 45, Santa Clara, Estado de México)	25	0.1
Cromato de Sodio ..... (Dow Chemical, México, D. F.)	120	0.1
Diesel ..... (PEMEX Mexico)	59500	64.7
Cemento Portland --- (México)	3000	3.2

Turbidity was estimated by the method and with the instruments of Jackson, using a turbidimeter 75 cm long. After each change of water in the aquaria, samples were taken for the measurements of turbidity, which was estimated twice in each sample. The maximum of turbidity decreased because of both the sedimentation of suspended material itself and the capacity of oysters to subtract suspended material from the water.

The aquaria were cleaned once a day by emptying them and scouring their walls and floor.

Chlorinity was estimated according to the method of Mohr-Knudsen, dissolved oxygen by the Winkler method, and temperature was taken with a Celsius thermometer. The frequency of these estimations was varied according to the conditions of each experiment; the minimum frequency was once every other day.

Nine experiments are considered in this article: two of a preliminary nature; three to estimate the effect of drilling fluids; three more to show the effect of some components of such drilling fluids in certain concentrations; and one experiment using natural mud.

In most of these experiments survival was observed in two samples—an experimental and a control sample—each containing 20 oysters.

One oyster was placed in each aquarium; a total of 320 oysters was used in these experiments. The experiments were run between March and August 1967, during periods when I had the opportunity to stay in the encampment.

## RESULTS

In figures 3 to 11 the results of the experiments are represented graphically. Figure 12 shows the index of 50% of oyster mortality in various concentrations of drilling fluids. Table 1 presents information on the variation of the environment in the aquaria.

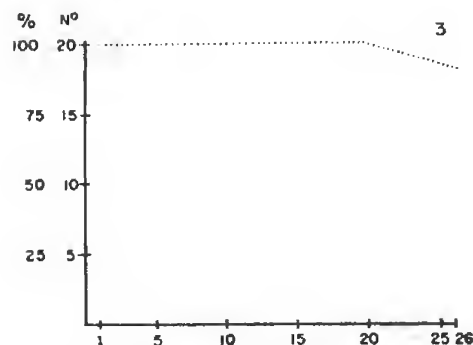


Fig. 3. After 26 days, during which the water was changed three times a day, 85% of the oysters had survived, showing a high index of survival. The ordinate shows the percentage and number of survivors; the abscissa the number of days tested.

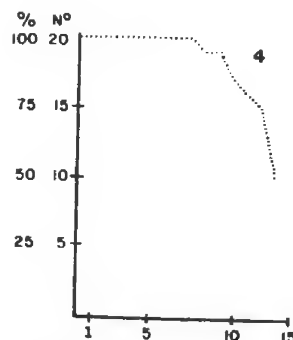


Fig. 4. Mortality was high when water was not changed; 50% survival was reached after 14 days. In the ordinate, survival; in the abscissa, time.



*Preliminary experiments.* A first experiment was conducted to obtain information on oyster survival under the optimum conditions of changing water which could be maintained for a long time; this would give an index of high survival. A second experiment, without changing the water, was set up to get an index of low survival, in contrast with the first.

After 26 days of the first experiment, during which the water was changed three times a day as mentioned above, 85% of the oysters had survived (fig. 3). This percentage was considered a sufficiently high index of survival, so this frequency of changing water was judged adequate for running the subsequent experiments.

The second experiment shows that 50% mortality was reached after 14 days (fig. 4); this was considered a low index of survival, as it showed that mortality could be high if the water were not changed.

*Effects of the drilling fluid.* Three experiments were established to test the effects of three different ranges of turbidity and of the drilling fluid.

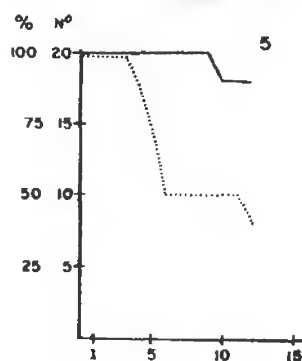


Fig. 5

Survival of two samples, the experimental (dotted line) and the control (continuous line). The first one was treated three times a day with drilling fluid up to 1000 to 2000 ppm of initial turbidity; 50% mortality was reached on the sixth day. In the ordinate, survival; in the abscissa, time.

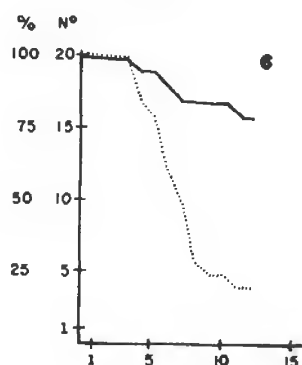


Fig. 6

Survival of two samples, the experimental (dotted line) and the control (continuous line). The first one treated three times a day with drilling fluid in initial turbidity between 200 and 500 ppm. 50% mortality occurred on the seventh day. In the ordinate, survival; in the abscissa, time.

The substances were used in the same form in which they are sold commercially. The concentration of each was arbitrary, always starting from the same volume of dry material suspended or dissolved in a given volume of water. As the properties of each substance are different in regard to solubility and suspensibility, the resulting turbidity was different for each component.

Tanino in turbidity between 90 and 170 ppm: 50% mortality was reached between the fourth and the fifth day in the experimental sample; mortality was total on the seventh day. The controls only reached 20% mortality on the seventh day (fig. 8).

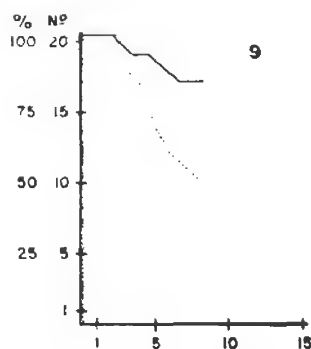


Fig. 9.

Survival of two samples, the experimental (dotted line) and the control (continuous line). The first one treated three times a day with Bentonita in initial turbidity between 110 and 190 ppm. 50% survival occurred on the eighth day. In the ordinate, survival; in the abscissa, time.

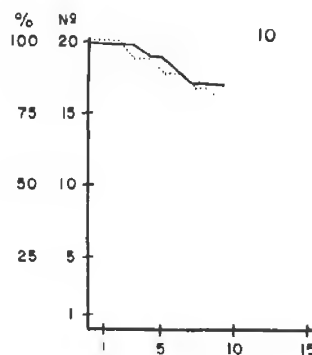


Fig. 10.

Survival of two samples, the experimental (dotted line) and the control (continuous line). The first one treated three times a day with Barita in initial turbidity between 50 and 65 ppm. Both survival curves were quite similar, so that no lethal effect was shown. In the ordinate, survival; in the abscissa, time.

Bentonita in concentrations between 110 and 190 ppm: 50% survival in the experiment sample occurred on the eighth day; at this time the control lot reached 20% mortality (fig. 9).

Barita in concentrations between 50 and 65 ppm: on the ninth day, survival was 80% in the experimental sample and 85% in the control. The survival curves were quite similar, so that no lethal effect was shown (fig. 10).

Daugherty (1951) reported some results on the action of Tanino, called in his paper "tannex"; he established that one lot of 24 oysters survived 22.5 hours in increased concentrations up to 140 ppm in a system with recirculating water and constant turbidity, and also found that a similar lot survived 20.5 hours in increased concentrations up to 450 ppm. From this the author concluded that tannex was not toxic to oysters; however, he proved that it is toxic to other marine organisms in concentrations of 70 to 450 ppm over the same period of time. Apparently the results of Daugherty and those presented in this article are not in agreement, but what caused the difference is probably the methodology. The main factor may be the length of time the experiment was run; however, the concentrations used and their variations, and the frequency of changing the water in the aquaria, also may be significant factors. In my opinion, Daugherty's experiments did not last long enough to show any mortality of oysters.

The Bentonita in 110 to 190 ppm proved to cause significant mortality in the experiment here reported; but in the opinion of the experts of Pemex this substance forms compounds of high density in the drilling fluid, so that its suspensibility is not great and it could not be scattered over a broad area in sufficient concentration at one time, to produce a significant mortality in the Laguna de Tamiahua. This opinion is supported and discussed also by Villalobos *et al.* (1968) referring to the total drilling fluid.

Daugherty (1951) reported that the "aquagel," a trade name for a high quality Bentonita, did not kill any oysters during 22 hours in concentrations as high as 7500 ppm. This author considered "aquagel" as non-toxic to marine animals. As in the case of the Tanino, the results obtained in the present experiments are apparently in disagreement with Daugherty's. The same major objection applies again: Daugherty's did not last long enough to kill the animals.

The Barita in the concentrations used in this experiment did not produce any apparent mortality as can be seen from the survival curves (fig. 10). In this respect Daugherty (1951) using "baroyd," made of selected Barita, also found this substance to be non-toxic either to the oyster or to the other marine animals of his experiments. Our findings are in agreement despite differences in methodology.

It is interesting to add that Daugherty (1950) found "sodium acid pyrophosphate" to be toxic to oysters in concentrations of 500 ppm and greater. This substance was not tested in our experiments.

In my opinion none of the information reported by Daugherty (1950-1951) or such of the present articles as concerns

the effect of components of the drilling fluid, could be applicable to the case of the Laguna de Tamiahua, as none of these substances was spilled in its commercial form; rather, they were used as components of the drilling fluid which was then used in the drilling, and it was only at the end of the drilling operations that the fluid was spilled. For these reasons it is assumed that the only information available that could be applicable to the case of the Laguna de Tamiahua is that presented herein referring to the effect of the drilling fluid upon the oysters. The applicability of this information, however, is not so obvious, and even it may be of doubtful value for many reasons. The most important of these reasons is that the laboratory experiments are not a complete reproduction of what happened at the time when the drilling fluids were spilled. Furthermore these experiments deal only with oysters and drilling fluid, without taking into consideration the whole ecosystem of which the oysters were a component; the drilling fluid, as a foreign substance, probably affected the usual functioning of the ecosystem, but at present no information is available on this difficult and complex problem. What is most desirable is to avoid the spilling of any foreign substance into coastal lagoons such as Tamiahua, without limiting the activities of the oil industry and other industries. This despite the opinion of Daugherty (1951) that the compounds tested, for him, were sufficiently low in toxicity to be of little danger when released in open bay waters.

As to the effect of natural mud on the survival of oysters, the high survival of the experimental lot in contrast with the controls, seems to show that this substance favors survival. Mackin and Hopkins (1962) pointed out that in certain localities in Louisiana, natural mortality of oysters was in inverse proportion of the water's turbidity; in places and periods with high turbidity, the mortality was lower. These results are in agreement with mine, but the reasons for this effect are not clear.

During the experiments variations were recorded in temperature, chlorinity and the concentrations of dissolved oxygen. This information did not require special treatment so only the limits were reported (Table 1). Temperature varied from 23° to 30°C, as a result of seasonal variations from spring to summer. Chlorinity varied between 4.40 and 16.57‰. Lower values were found during a short period in August in relation to the rainy season in summertime.

The concentrations of dissolved oxygen varied between 3.0 and 7.6 ml/L; it was highest during the intake of water. Low values of oxygen were found only at the end of the second experiment, probably due to fermentation and oxidation in the stagnant water. It seems logical to believe that temperature,

chlorinity and dissolved oxygen fluctuated between narrow limits so as to give comparable results in the various experiments.

Availability of food was not controlled, but it seems that oysters can survive long periods without abundant food, according to experiments conducted by Dr. Sammy M. Ray (personal communication).

### CONCLUSIONS

Drilling fluid reduced the survival of oysters significantly in concentrations of over 200 ppm in laboratory aquaria. In turbidities between 200 and 500 ppm, 50% mortality was reached on the seventh day. According to Villalobos *et al.* (1968), these concentrations could hardly be maintained in time and space sufficient to produce significant mortality or the claimed extermination of the oyster reefs in the Laguna de Tamiahua.

This conclusion is the only one that could be applicable to the case of the Laguna de Tamiahua, as all the others deal with commercial components of the drilling fluid, and these were not spilled as components. Nothing is known about the effect of drilling fluid upon the ecosystem to which oysters belong.

Tanino in concentrations between 90 and 170 ppm had a drastic effect upon survival, which was 50% between the fourth and fifth days.

Bentonita in 110 to 190 ppm resulted in 50% survival on the eighth day.

Barita in concentrations between 50 and 65 ppm did not produce noxious effects on the survival of the oysters.

Natural mud in concentrations from 200 to 500 ppm was favorable for the survival of oysters.

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# Gulf Research Reports

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Volume 3 | Issue 2

---

January 1971

A Bibliography of Anomalies of Fishes, Supplement 2

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DOI: 10.18785/grr.0302.05

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# A BIBLIOGRAPHY OF ANOMALIES OF FISHES

## Supplement 2

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This listing adds 213 titles to the original bibliography (Gulf Res. Repts. 1(6), 1964) and the 1966 supplement (Gulf Res. Repts. 2(2):169-176). Although a number of previously overlooked references are included, there are 137 citations of works published during the 1965-70 period. The frequency of recent publications offers some indication of the current worldwide interest in problems of fish teratology.

Apparently in response to increased interest in the environment, some American authors are now attempting to relate anomalies in natural or "wild" populations of fishes to pollution levels. While this may be a useful area of investigation, the results should be evaluated with caution. It is obvious that only sub-lethal conditions are observed and there are few data, especially in marine or estuarine environments, upon which to establish a "normal" survival potential for a particular abnormality in any species. Those hoping to use published records to establish a "base-line" should bear in mind that, with few exceptions, both old and recent publications report only the most obvious and striking conditions (macro-anomalies). Investigators attempting to determine frequencies of abnormalities should include data on the less obvious and possibly very common micro-anomalies.

This supplement includes an Index of Sources and Abbreviations covering those journals not included in the original bibliography. As in the previous supplement, titles are serially numbered and prefixed by the letter "S"; the prefix has been omitted from the index listings. Corrections to be made in the original bibliography are indicated under Corrigenda.

I again wish to express my continuing appreciation to those colleagues who have provided reprints of their papers or otherwise contributed to this bibliography.



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#### TAXONOMIC INDEX

- Abramis ballerus* — 295.  
*Acipenser guldenstaedti* — 303.  
*Acrocheilus alutaceus* — 239.  
*Alburnoides bipunctatus* — 222.  
*Alosa pseudoharengus* — 149, 263.  
     *sapidissima* — 155, 163.  
*Amia calva* — 186.  
*Anchoa mitchilli* — 131.  
*Anguilla anguilla* — 301.  
     *bengalensis* — 198.  
     *japonica* — 192.  
*Anisotremus davidsonii* — 190.  
     *scapularis* — 178.  
*Anoplopoma fimbria* — 243.  
*Apistogramma ramirezi* — 260.  
*Barbus canis* — 241.  
*Basilichthys bonariensis* — 159.  
*Blicca bjoerkna* — 240.  
     *bjoerkna* — 295.  
*Boops salpa* — 122.  
*Bothus ovalis* — 270.  
*Brevoortia smithi* — 206.  
     *tyrannus* — 131, 206, 230, 296.  
*Carassius* — 260, 264, 268, 280, 282, 298, 299.  
     *auratus* — 173.  
     *auratus gibelio* — 207.  
*Carcharhinus limbatus* — 108.  
*Carcharodon carcharias* — 164.  
*Catostomus clarkii* — 93.  
     *columbianus* — 239.  
     *insignis* — 93.  
     *macrocheilus* — 239.  
*Ceratoptera ehrenbergii* — 105.  
*Channa punctatus* — 278, 279.  
*Chionoecetes opilio elongatus* — 195.  
*Chirocentrus nudus* — 202.  
*Chondrostoma nasus* — 249.  
*Citharichthys abbotti* — 139.  
*Clupea harengus* — 95, 109, 119, 157, 168, 185.  
     *pilchardus* — 210.



*Coregonus* — 167.  
*Cottus aleuticus* — 239.  
     *asper* — 239.  
     *confusus* — 239.  
     *rhotheus* — 239.  
*Cynoglossus lida* — 270.  
     *semifasciatus* — 266.  
*Cynoscion regalis* — 131.  
*Cynoscion nebulosus* (sic) — 262.  
*Cyprinus carpio* — 196.  
*Dasyatis sabina* — 131.  
*Diplodus vulgaris* — 285.  
*Drepane punctata* — 272.  
*Elassoma okefenokee* — 110.  
*Eleutheronema tetradactylum* — 237.  
*Elops saurus* — 131.  
*Esox* — 214, 295.  
     *lucius* — 100, 203, 204, 300.  
*Etheostoma olmstedii* — 304.  
*Etropus crossotus* — 131.  
*Fundulus heteroclitus* — 124, 166.  
*Gadella maraldi* — 126.  
*Gadus morhua* — 288.  
     *virens* — 133.  
*Galeichthys felis* — 131.  
*Galeorhinus zyopterus* — 128.  
*Gambusia affinis* — 118.  
*Gerres oyena* — 248.  
*Gila robusta* — 93.  
*Girella tricuspidata* — 297.  
*Gobio gobio* — 281.  
*Gobionellus hastatus* — 135.  
*Gobius microps* — 175.  
*Gymnura* — 148.  
     *micrura* — 131.  
     *poecilura* — 105.  
*Heterodontus japonicus* — 271.  
*Heteropneustes fossilis* — 101.  
*Hippocampus Hippocampus erectus erectus* — 302.  
*Holanthias chrysostictus* — 286.  
*Hyphessobrycon flammeus* — 156.  
*Hyporhamphus unifasciatus* — 140.  
*Ictalurus* — 221.  
     *punctatus* — 111.  
*Inopsetta ischyra* — 176.  
*Katsuwonus pelamis* — 217.  
*Lampetra lamottei* — 213.  
*Lebistes reticulatus* — 127, 151.  
*Lepisosteus platystomus* — 186.  
*Leporinus* — 162.  
*Limia melanogaster* — 290.

*Lota lota lacustris* — 103.  
*Lycengraulis barbouri* — 220.  
*Macrozoarces americanus* — 253.  
*Makaira* — 143.  
*Mastacembelus armatus* — 211.  
*Melanogrammus aeglefinus* — 253.  
*Menidia menidia* — 131, 182.  
*Menticirrhus americanus* — 131.  
*Merluccius esculentus* — 115.  
     *merluccius hubbsi* — 125.  
     *productus* — 223.  
*Microgobius gulosus* — 135, 137.  
*Micropogon undulatus* — 172.  
*Micropterus dolomieu* — 239.  
*Microstomus achne* — 184.  
*Morwong fuscus* — 297.  
*Mugil cephalus* — 224.  
*Notopterus notopterus* — 267.  
*Novadon modestus* — 183.  
*Oncorhynchus gorbuscha* — 161, 177.  
     *keta* — 161, 231.  
     *kisutch* — 129, 239.  
     *nerka* — 161.  
     *tshawytscha* — 158, 171, 239, 261.  
*Onos mediterraneus* — 287.  
     *sellai* — 287.  
*Oryzias latipes* — 275, 276.  
*Osmerus eperlanus* — 208.  
*Otolithus argenteus* — 174.  
*Pugrosomus auratus* — 251.  
*Paralabrax nebulifer* — 130, 291.  
*Paralichthys albigutta* — 181.  
     *dentatus* — 131.  
     *lethostigma* — 131, 136, 138, 227.  
*Perca flavescens* — 203.  
     *fluviatilis* — 216, 260.  
*Petromyzon marinus* — 213.  
*Phochilodus* — 123.  
*Piabucina festae* — 113.  
*Platichthys flesus* — 218.  
*Platygobio gracilis* — 187.  
*Pleuronectes platessa* — 293.  
*Pleuronichthys coenosus* — 238.  
*Poecilia velifera* — 188.  
*Polynemus heptadactylus* — 232.  
*Polyodon spathula* — 215.  
*Pomatomus saltatrix* — 265.  
*Pomoxis annularis* — 228.  
*Protopterus dolloi* — 104.  
*Pseudopleuronectes americanus* — 136.  
*Ptychoceilus oregonensis* — 239.

*Raja binoculata* — 117.  
     *clavata* — 179, 180, 258.  
     *eglanteria* — 131.  
     *richardsoni* — 154.  
*Rastrelliger kanagurta* — 99.  
*Reinhardtius hippoglossoides* — 283.  
*Remora remora* — 197.  
*Rhinichthys cataractae* — 239.  
     *osculus* — 239.  
*Rhinolepis aspera* — 226.  
*Rhynchobatus djiddensis* — 105.  
*Richardsonius balteatus* — 239, 261.  
*Roccus saxatilis* — 141, 255, 277.  
*Roeboides* — 242.  
*Rutilus rutilus* — 96.  
*Salmo* — 189, 247.  
     *gairdneri* — 120, 239, 260.  
     *trutta* — 229, 274.  
*Salvelinus fontinalis* — 239.  
     *malma* — 92.  
     *namaycush* — 209.  
*Sarda chiliensis* — 217.  
*Sardina pilchardus* — 246.  
*Sardinella longiceps* — 106, 107, 165, 294.  
*Scardinius erythrophthalmus* — 112.  
*Schizothorax niger* — 212.  
*Scoliodon walbeehmi* — 98.  
*Scolopsis phaeops* — 256.  
*Scomber scombrus* — 170.  
*Scomberomorus maculatus* — 102.  
*Scophthalmus maeoticus* — 250.  
*Scylliorhinus caniculus* — 199.  
*Scylliorhinus canicula* — 260.  
*Scyllium stellare* — 292.  
*Sebastes oblongus* — 235.  
*Sebastodes aleutianus* — 244.  
     *alutus* — 244.  
     *crameri* — 244.  
     *elongatus* — 244.  
     *entomelas* — 244.  
     *flavidus* — 152, 245.  
     *melanostomus* — 153.  
     *miniatus* — 244.  
     *paucispinis* — 134, 244, 245.  
     *pinniger* — 244, 245.  
     *rubrivinctus* — 244.  
*Sebastolobus macrochir* — 191.  
*Segutilum sydneyanum* — 297.  
*Solea lascaris nasuta* — 144.  
     *vulgaris* — 236.

*Somniosus pacificus* — 128.  
*Sphyrna lewini* — 219.  
     *zygaena* — 128.  
*Spirinchus* — 145.  
*Stellifer lanceolatus* — 131.  
*Stizostedion lucioperca* — 252.  
*Strinsia tinca* — 126.  
*Symphurus diomedianus* — 225.  
     *plaginsa* — 131.  
*Tarpon atlanticus* — 233.  
*Tautoga onitis* — 116.  
*Trachurus symmetricus* — 146.  
*Trachysurus dussumieri* — 254.  
*Trichiurus lepturus* — 273.  
*Trinectes maculatus* — 131, 136, 138.  
*Urophycis regius* — 131.  
*Xiphophorus* — 97.  
     *helleri* — 150, 234.  
     *maculatus* — 94.

#### INDEX OF ANOMALIES

Abnormal coloration — 100, 111, 131, 134, 156, 174, 177, 187,  
     217, 234, 238, 243, 293.  
 Albinism — 94, 101, 130, 136, 153, 186, 191, 196, 198, 219, 221,  
     226, 236, 254, 260, 293.  
 Ambicoloration — 131, 138, 181, 193, 225, 236, 270, 293.  
 Anal fin — 256, 294.  
 Barbels — 165.  
 Body (misc.) — 95, 99, 102, 108, 162, 187, 192, 205, 213, 239,  
     269, 301.  
 Caudal fin, etc. — 107, 126, 131, 144, 233, 239, 286, 294.  
 Dorsal fin, etc. — 137, 147, 167, 288.  
 Eye — 115, 141, 209, 228, 241, 252, 277.  
 Fins (misc.) — 108, 110, 131, 147, 173, 194, 204, 229, 260, 264,  
     282.  
 Gills, etc. — 98, 108, 189, 281, 282, 291, 298, 304.  
 Head (misc.) — 121, 143, 145, 147, 185, 239, 285, 287, 289, 291.  
 Internal organs, fasciae, etc. — 268.  
 Lateral line, etc. — 146, 151, 160, 167, 176, 222.  
 Melanalbinism — 138, 153.  
 Melanism — 97, 109, 152, 153, 188, 189, 215, 218, 244, 245, 247,  
     297.  
 Mouth, jaws, etc. — 131, 135, 274, 285, 299.  
 Pectoral fin, etc. — 104, 105, 148, 200, 240, 300.  
 Pelvic fin, etc. — 132, 178, 220, 239, 240, 278, 280, 281, 282, 291.

Pug-head, etc. — 116, 131, 147, 163, 203, 214, 216, 235, 252, 253, 255, 259, 260, 262, 277, 296.  
 Regeneration — 107, 126, 127, 165, 166, 173, 280.  
 Reversal — 139, 225, 227, 266.  
 Scales, etc. — 135, 136, 187, 281.  
 Sex organs, hermaphroditism, etc. — 92, 96, 106, 118, 119, 123, 124, 125, 142, 149, 150, 155, 157, 168, 180, 199, 207, 208, 211, 212, 223, 224, 231, 232, 237, 246, 248, 263, 267, 279, 284, 290, 292.  
 Teeth, etc. — 128.  
 Triple monsters — 120.  
 Twins, double monsters, etc. — 147, 210, 260, 271, 302, 303.  
 Vertebral — 93, 103, 122, 126, 131, 135, 136, 147, 159, 161, 167, 171, 172, 175, 182, 183, 189, 201, 206, 222, 230, 239, 242, 247, 249, 251, 257, 260, 272, 273, 275, 276, 283, 291, 294, 301.  
 Wounds — 112, 113, 114, 117, 131, 133, 140, 147, 154, 158, 164, 169, 170, 197, 202, 209, 233, 250, 261, 265, 277, 288.  
 Xanthochroism — 138, 184, 190, 297.

#### INDEX OF SOURCES AND ABBREVIATIONS

Acta biol. cracov. Zool.—Acta Biologica cracoviensia. Kraców.  
 Advan. Mar. Biol.—Advances in Marine Biology. Academic Press, N. Y.  
 An. Congr. Lat-Amer. Zool.—Anais do Congresso Latino-Americana de Zoologia. São Paulo.  
 Ann. Fac. Sci. Univ. Dakar—Annales de la Faculté des sciences, Université de Dakar.  
 Ann. Mus. Stor. nat. Genova—Annali del Museo civico di storia naturale. Genova.  
 Ann. Parasit. hum. comp.—Annales de parasitologie humaine et comparée. Paris.  
 Arch. Environ. Health—Archives of Environmental Health. London.  
 Arch. FischWiss.—Archiv für Fischereiwissenschaft. Hamburg.  
 Arg. Estac. Biol. mar. Univ. Ceara—Arquivos. Estacao de Biologia Marinha. Universidad do Ceará. Fortaleza.  
 Bol. Soc. Cear. Agron.—Boletim da Sociedade cearense de agronomia. Ceara.  
 Bull. Bingham oceanogr. Coll.—Bulletin of the Bingham Oceanographic Collection. New Haven, Conn.  
 Bull. Cent. Etude Rech. sci., Biarritz.—Bulletin du Centre d'études et de recherches scientifiques. Biarritz.

- Bull. Mar. Sci.—Bulletin of Marine Science. Miami, Fla.
- Bull. mens. Soc. linn. Lyon.—Bulletin Mensuel de la Société Linnéenne de Lyon. Lyon.
- Bull. Misaki Mar. biol. Inst.—Bulletin of the Misaki Marine Biological Institute. Kyoto University. Kyoto.
- Bull. Pacif. Mar. Fish. Comm.—Bulletin of the Pacific Marine Fisheries Commission. Portland, Ore.
- Bull. U. S. Nat. Mus.—Bulletin of the United States National Museum, Washington, D. C.
- Caca e Pesca—Caca e Pesca. São Paulo.
- Ciênc. e Cult.—Ciência e Cultura. Revista da Sociedade Brasileira para o Progresso da Ciência. São Paulo.
- Contr. Fish Comm. Ore.—Contributions. Oregon Fish Commission. Portland, Ore.
- Contr. Sch. Fish. Univ. Wash.—Contributions. School of Fisheries. University of Washington. Seattle, Wash.
- Contr. Sci. Los Angeles Cty. Mus.—Contributions in Science. Los Angeles County Museum. Los Angeles, Calif.
- Crustaceana—Crustaceana. Leiden.
- Csl. Rybárst.—Ceskoslovenské Rybárstvi. Prague.
- Dopov. Akad. Nauk. ukr. RSR—Dopovidi Akademiyi nauk Ukrayins'koyi RSR. Kiev.
- Drum and Croaker—Drum and Croaker. Palos Verdes, Calif.
- Embryologia, Nagoya—Embryologia. Nagoya University. Nagoya.
- Fauna, Oslo—Fauna. Norsk Zoologisk Tidsskrift. Oslo.
- Fischereiwelt—Fischereiwelt. Hamburg.
- Fischwirtschaft—Fischwirtschaft. Bremmerhaven.
- Gerontologia—Gerontologia. Basel, N. Y.
- Invest. pesq.—Investigación pesquera. Barcelona.
- Israel J. Zool.—Israel Journal of Zoology. Tel Aviv.
- J. Miss. Acad. Sci.—Journal of the Mississippi Academy of Sciences. Jackson, Miss.
- J. Parasit.—Journal of Parasitology. Lancaster, Pa.
- J. Zool., London—Journal of Zoology. London.
- London Nat.—London Naturalist. London.
- Lucrar. Stat. zool. mar. Agigea—Lucrarile ale Statiei zoologice maritime 'Regele Ferdinand I' della Agigea.
- Mem. Ist. ital. Idrobiol. de Marchi—Memorie dell'Istituto Italiano di Idrobiologia Dott. Marco de Marchi. Milano.

- Nat. Wales—Nature in Wales. Orielson.
- Notas Estud. Inst. Biol. marit.—Notas e estudos do Instituto de biologia maritima. Lisbon.
- Notul. nat. Acad. Philad.—Notulae Naturae. Academy of Natural Sciences of Philadelphia. Philadelphia, Pa.
- N. Y. Fish Game J.—New York Fish and Game Journal. Albany, N. Y.
- Opusc. zool. Inst. zoosyst Univ. budapest—Opuscula Zoologica. Instuti Zoosystematici Universitatis Budapestinensis. Budapest.
- Pacific Sci.—Pacific Science. Honolulu, Hi.
- Pakist. J. Sci. indust. Res.—Pakistan Journal of Science and Industrial Research. Karachi.
- Physis. B. Aires—Revista de la Sociedad argentina de ciencias naturales. Buenos Aires.
- Proc. biol. Soc. Wash.—Proceedings of the Biological Society of Washington. Washington, D. C.
- Proc. Calif. Acad. Sci.—Proceedings of the California Academy of Sciences. San Francisco, Calif.
- Proc. Conf. stheast. Ass. Game Commrs.—Proceedings of the Annual Conference of the Southeastern Association of Game and Fish Commissioners. Columbia, S. C.
- Proc. int. Congr. Zool.—Proceedings of the International Congress of Zoology. London.
- Proc. Leeds phil. lit. Soc.—Proceedings of the Leeds Philosophical and Literary Society. Leeds.
- Proc. Mont. Acad. Sci.—Proceedings of the Montana Academy of Sciences. Missoula, Mont.
- Proc. nat. Acad. Sci. India—Proceedings of the National Academy of Sciences of India. Allahabad.
- Przegl. Zool.—Przegląd Zoologiczny. Warsaw.
- Publ. Serv. Piscic. Bras.—Publicações. Servico de piscicultura, Brasil. Fortaleza.
- Publs. Carnegie Instn.—Publications of the Carnegie Institution of Washington. Washington, D. C.
- Quart. J. Fla. Acad. Sci.—Quarterly Journal of the Florida Academy of Sciences. Tallahassee, Fla.
- Res. Briefs—Research Briefs. Oregon Fish Commission. Portland, Ore.
- Res. Bull. Punjab Univ. Sci.—Research Bulletin of the Punjab University of Science. Hoshiarpur.

- Rev. Trav. Inst. Pêche. marit.—Revue des Travaux de l'Institut des Pêches. Maritimes. Paris.
- Rev. Trav. Off. Pêche. marit.—Revue des Travaux de l'Office des Pêches Maritimes. Paris.
- Schr. naturw. Ver. Schlesw.-Holst.—Schriften des Naturwissenschaftlichen Vereins für Schleswig-Holstein. Kiel.
- Scot. Fish. Bull.—Scottish Fisheries Bulletin. Edinburgh.
- Skr. Komm. Havunders.—Skrifter udg. of Kommissionen for Havundersogelser. Copenhagen.
- Texas J. Sci.—Texas Journal of Science. Houston, Tex.
- Tijdschr. ned. dierk. Ver.—Tijdschrift der Nederlandse Dierkundige Vereeniging. Leiden.
- Trav. Sebast. biol. Sta.—Trudŷ Sevastopol'skoï biologicheskoi stantsii Akademiya nauk SSSR.
- Trop. Fish Hobbyist—Tropical Fish Hobbyist. Jersey City, N. J.
- Trud. Inst. Biol. Vodokhr.—Trudŷ Instituta biologii vodokhranilishch. Akademiya nauk SSSR. Moskow.
- Underw. Nat.—Underwater Naturalist. Bulletin of the American Littoral Society. Highlands, N. J.
- Vet. Rec.—Veterinary Record. London.
- Wassman J. Biol.—Wassman Journal of Biology. San Francisco, Calif.
- Zool. Polon.—Zoologica Poloniae. Breslau.
- Zool. Zh.—Zoologicheskii zhurnal. Moskow.

#### CORRIGENDA

The following corrections should be entered in the appropriate sections of the original bibliography (Gulf Res. Repts. vol. 1, no. 6).

Reference	Correction
Title 447	To read: 40 (4) :564-571
" 561	Change: "rav" to ray
" 681	Change date to: 1903
" 925	To read: 27:263-264
" 953	To read: myctéridoide
" 993	Add: Univ. Paris (A) 244:1-179, 26 figs.
" A 15	To read: (Cuvier)
Page 371	To read: <i>Katsuwonus pelumys</i> — 465.
" 374	Syngnathidae: add—194, 195.
" 376	Pug-head, etc.: delete—555.
" 385	Collect. & Breed.: add—saishu to siiku



# Gulf Research Reports

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Volume 3 | Issue 2

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January 1971

Descriptions of Shrimp Larvae (Family Penaeidae) Off the Mississippi Coast

Chebium B. Subrahmanyam

*Gulf Coast Research Laboratory*

DOI: 10.18785/grr.0302.06

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DESCRIPTIONS OF SHRIMP LARVAE  
(FAMILY PENAEIDAE) OFF THE MISSISSIPPI COAST

by  
C. B. Subrahmanyam<sup>1</sup>

INTRODUCTION

Müller (1864) showed that the penaeid egg hatches into a nauplius. Some years later studies of the metamorphosis of penaeid shrimps in the Gulf of Mexico were made (Pearson 1939, Heegaard 1953, Dobkin 1961, Cook and Murphy 1965, and Renfro and Cook 1963). The present paper treats the larvae taken in Mississippi and brings together the descriptions of the larvae scattered in the literature. The salient features of various stages of different species of the six genera studied are pointed out with the aid of drawings to facilitate easier identification. Besides the references cited above, the works of Heldt (1938), Gurney (1924, 1942), Heegaard (1966) and Cook (1966) have been consulted for this presentation.

The author is grateful to Dr. Gordon Gunter for his helpful criticisms and to Dr. Harold Howse, Gulf Coast Research Laboratory, for his generous help in photography.

MATERIALS AND METHODS

Plankton was collected simultaneously from the surface, mid-depth, and bottom at 10 m, 18 m, 36 m, 54 m, 72 m, and 90 m depths in the Gulf of Mexico. The nets used were fitted with closing devices and the netting had a mesh of 0.33 mm. After letting the plankton settle, penaeid larvae were picked out of the entire sample and preserved in buffered 5% formalin.

Photographs were taken with the aid of a microprojector. The larvae were placed in a depression slide which was mounted on the stage of the projector. The image of the specimen was directly focussed on an 8.3 x 10.2 cm photographic plate in a dark room and processed immediately. The subjects were printed on a high contrast gloss paper (Kodabromide F-5). Magnifications were measured by photographing a stage micrometer under the same setting. This method permits greater freedom for focussing and greater resolution of the objects. Pictures were drawn based on these photographs.

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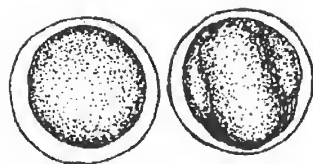


FIG. 1

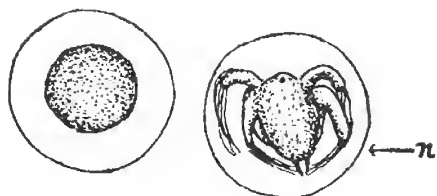


FIG. 2

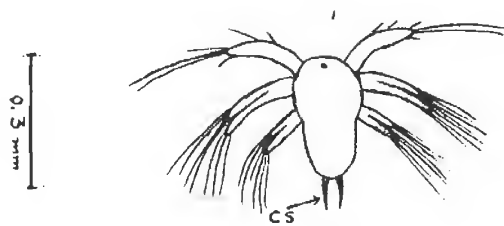


FIG. 3

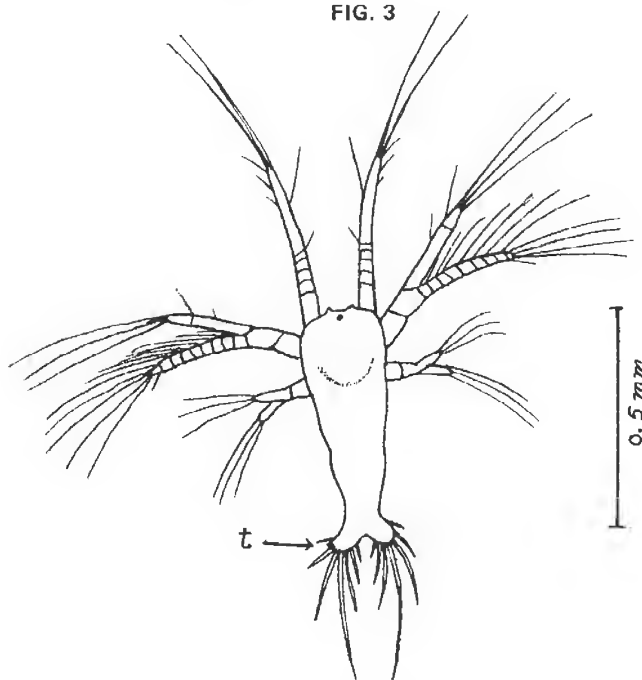


FIG. 4

The six littoral genera encountered in the samples were *Penaeus*, *Parapenaeus*, *Trachypeneus*, *Xiphopeneus*, *Sicyonia*, and *Solenocera*. Some larvae of *Gennadus* and *Artemisia* were taken one day in two years of collecting, and they are described separately (Subrahmanyam and Gunter 1970).

## THE LARVAE

### Eggs

*Penaeus* (Fig. 1). The egg measures 0.33 mm in diameter. The egg membrane is transparent. The perivitelline space is narrow and the embryo occupies almost the entire inside of the egg.

*Trachypeneus* (Fig. 2). Eggs with embryonic mass and nauplii inside measure 1.38 mm in diameter. They are larger than *Penaeus* eggs and the perivitelline space is wider. The nauplius, however, fills up the egg. These eggs were taken in thousands on some occasions.

### Nauplius

*Penaeus* (Fig. 3). Only nauplius V of this genus was collected. It measured 0.55 mm in body length. The oblong pear shaped body, deeply notched telson lobes, and long setae on the appendages are characteristic. These were collected mostly from 36 to 54 meter stations, and could belong to the white or brown shrimp.

*Trachypeneus* (Fig. 4). Only nauplius I of this genus was collected. It measures 0.28 mm in body length. The oval body and a protuberance on the dorsal side of the larva posterior to the median eye distinguish this larva. The eggs and nauplii of this genus were collected mostly at 9, 18, and 36 meter stations.

### Protozoa

*Penaeus* (Fig. 5). Protozoa I measured 0.90 mm in body length. Frontal organs are present. The formula for the lateral setae on the end pod of antenna II is  $2 + 2 + 1$  (Fig. 5A). The second protozoa (Fig. 5B) measures 2.04 mm in length. The rostral spine is long, ventrally curved, and measures about one third of the carapace length. Supraorbital spines are present. Protozoa III (Fig. 5C) measures 3.04 mm. The rostrum is longer. The lateral setae on the second antennal endopod retain the same formula as protozoa I.

*Trachypeneus* (Fig. 6). Protozoa I measures 0.91 mm in body length. It is very delicate and transparent (Fig. 6A). Protozoa II measures 1.40 mm in body length. The rostrum is

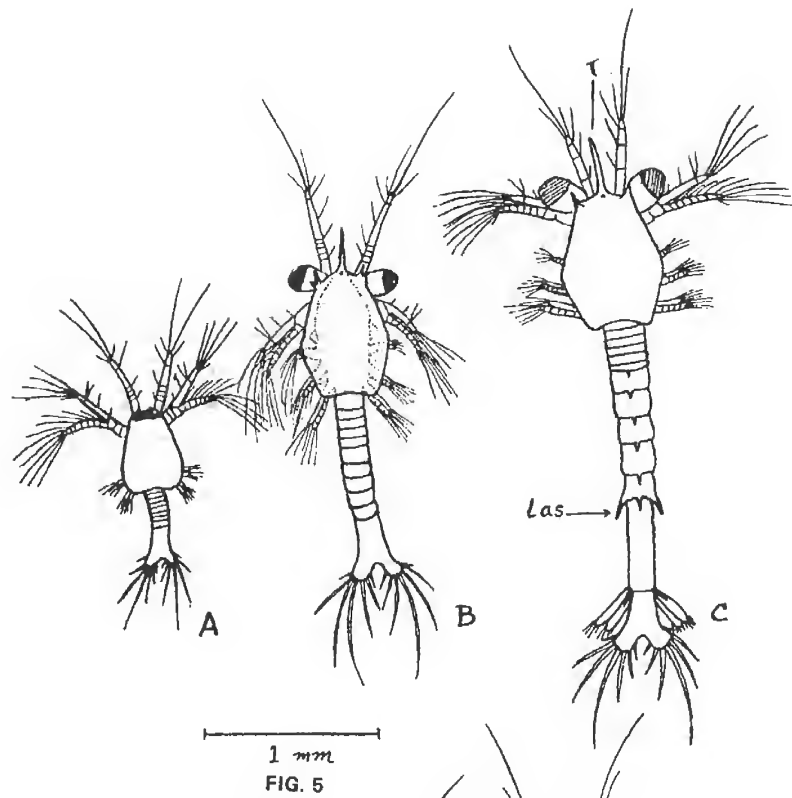


FIG. 5

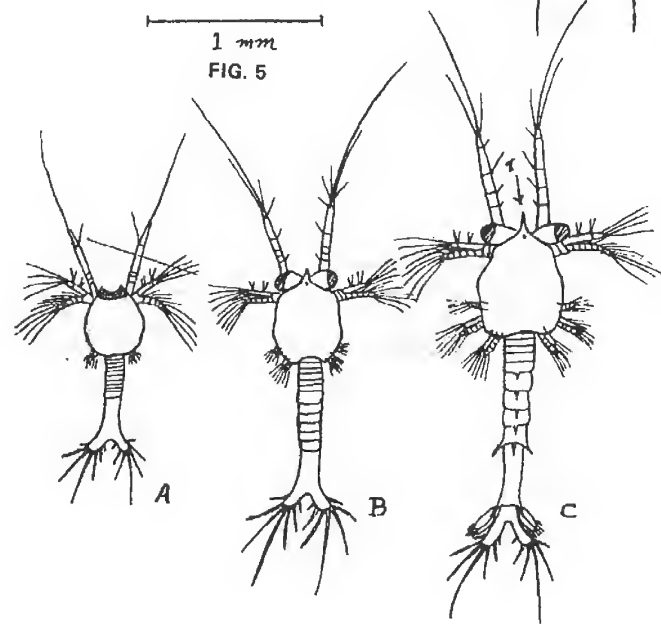
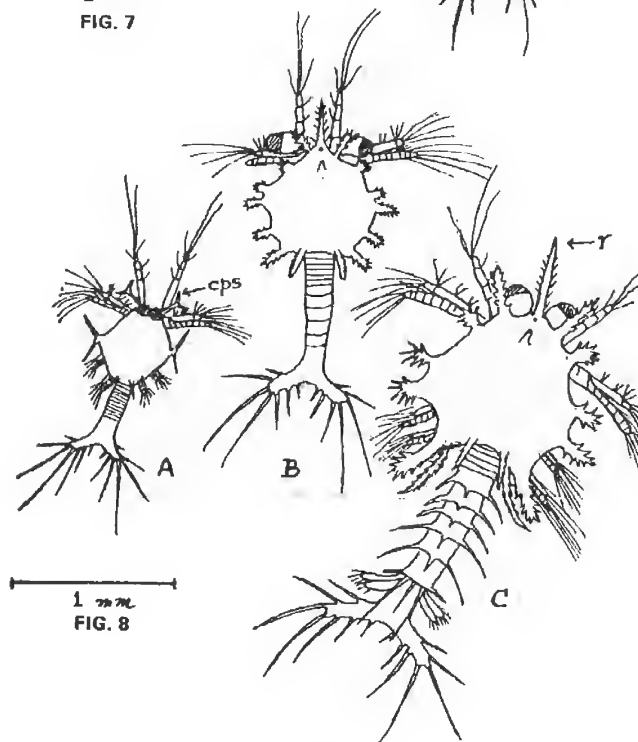
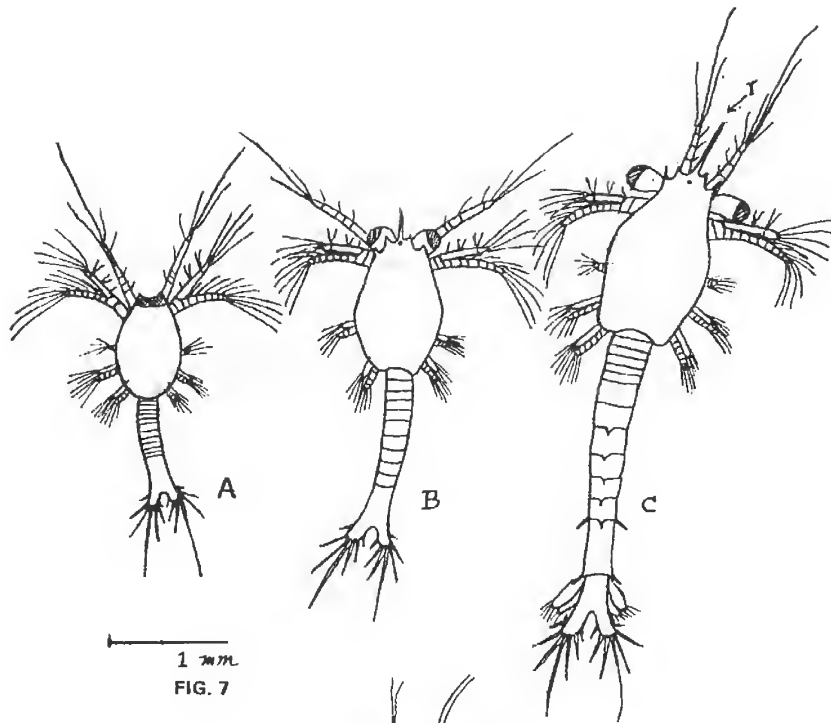


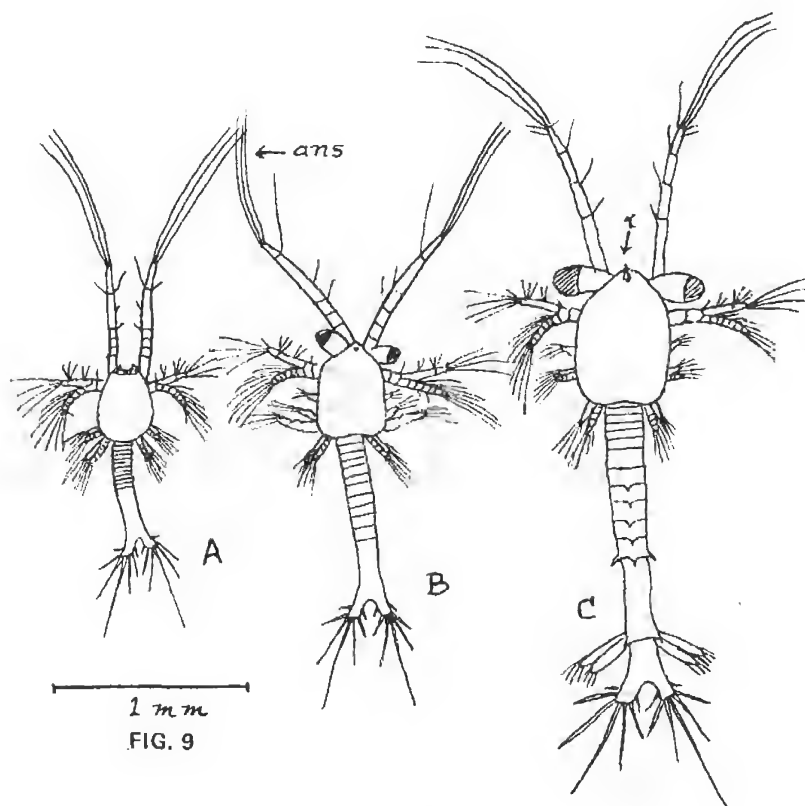
FIG. 6



short, and supraorbital spines are absent (Fig. 6B). Protozoa III measures 1.97 mm in body length. The rostrum is short (Fig. 6C). All three stages are identifiable with the setal formula of the second antennal endopod, 2 + 2, and short rostrum in second and third stages.

*Xiphopeneus*. The protozoal stages of this genus are identical in morphology and sizes to those of *Trachypeneus* except for one short terminal setae on the second antennal endopod.

*Parapeneus* (Fig. 7). Protozoa I is larger than the other genera. It measures 1.28 mm in length (Fig. 7A). This stage and the following two stages show 2 + 2 + 1 lateral setae on the second antennal endopod. Protozoa I (Fig. 7B) measures 2.04 mm and is robust. The rostrum extends to the distal segment of first antenna, and two pairs of supraorbital spines are present. The third protozoa (Fig. 7C) measures 3.18 mm in body length. The rostrum is longer than that of comparable stage of *Peneus*.



*Solenocera* (Fig 8). Protozoa I (Fig. 8A) measures 1.0 mm in length. It has a short rostrum even at this stage. The carapace carries forked spines above the eyes, laterally and dorsally at the junction of carapace. The telson lobes are large and the notch is very shallow. The formula for the lateral setae on the second antennal endopod is  $2 + 2 + 3$  for all the three stages. The second protozoa (Fig. 8B) measures 1.84 mm in body length. The rostrum is spiny and as long as the first antenna. The carapace is characterized by spiny lobes. The eyes are large. The third protozoa (Fig. 8C) measures 2.66 mm in body length. It is robustly built, and the rostrum is longer than the first antenna. The supraorbital spines are large and robust. The carapace shows accentuated spiny protrusions and it is spiny all over. The salient feature is the presence of lateral spines on all the six abdominal segments. The telson carries long spines.

*Sicyonia* (Fig. 9). The first protozoa measures 0.93 mm in body length. The striking feature is the long first antenna (longer than the second) with three long terminal setae (Fig. 9A). The formula for the lateral setae on the endopod of second antenna is  $3 + 2 + 1$ , which is the same for the next two

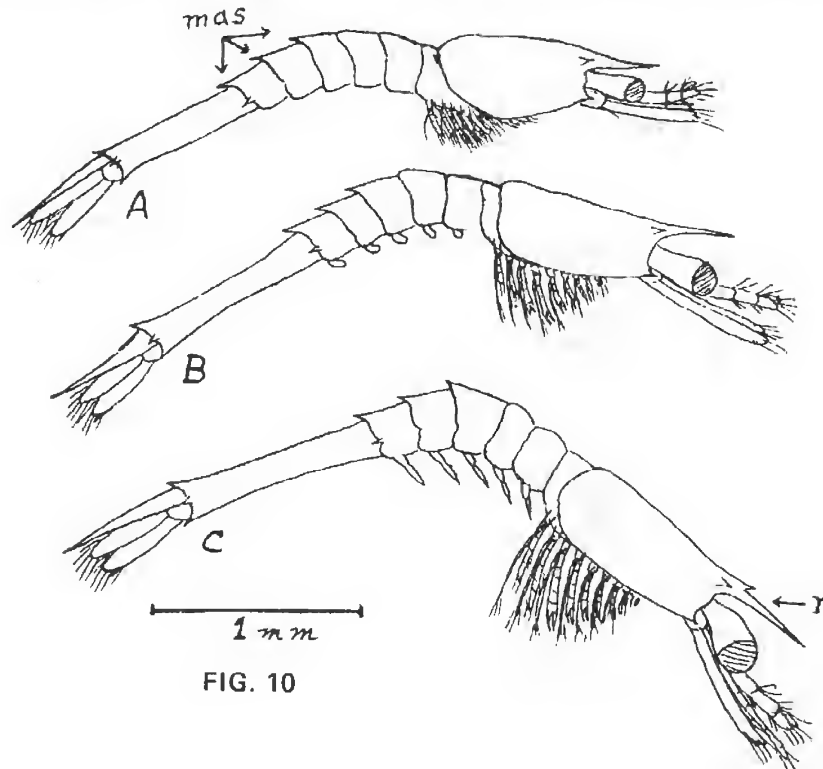
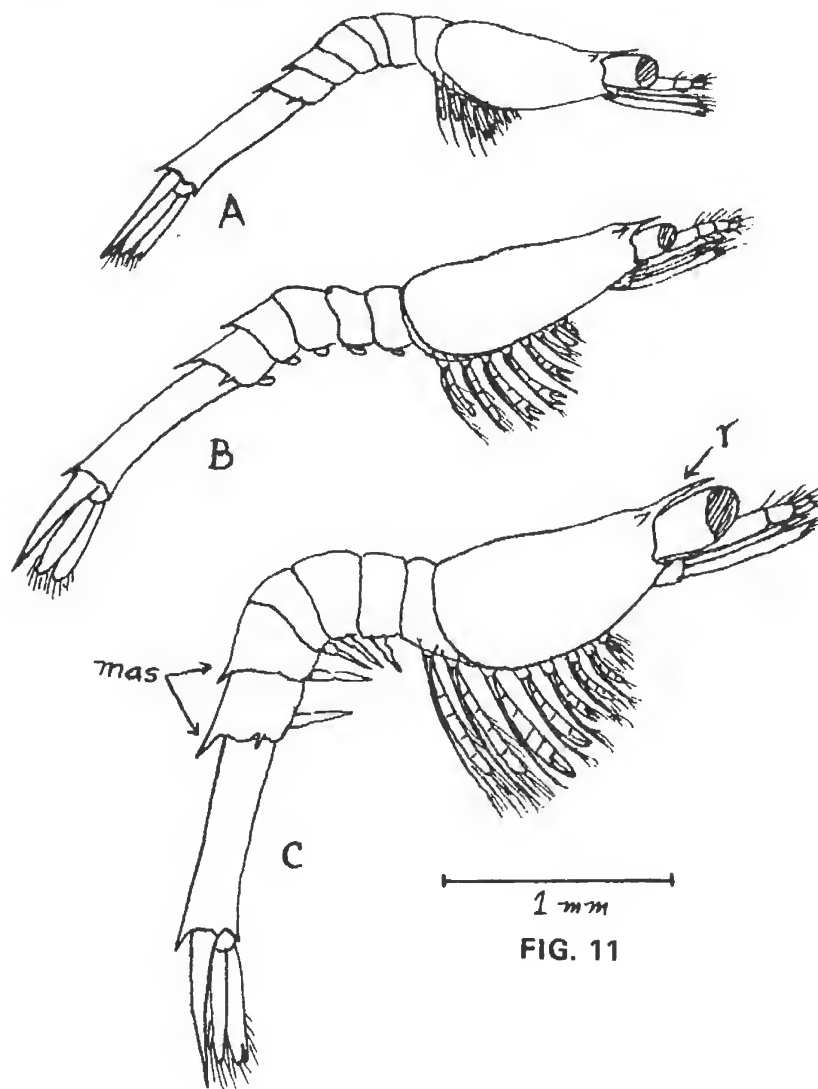


FIG. 10



stages. The notch on the telson is narrower than that of *Penaeus* and *Trachypeneus*. The second protozoea is characterized by the absence of rostrum (Fig. 9B). It measures 1.42 mm in body length. The first antennae are still the longest appendages. The third protozoea also shows no rostrum (Fig. 9C). This larva measures 2.24 mm in body length. It can be distinguished from the other genera by the three long antennal setae and the narrow notch on the telson.



## Mysis

*Penaeus* (Fig. 10). All three mysis stages can be identified by the length of the rostrum reaching beyond the eyes, and dorsally one small spine each on the third, fourth, and fifth abdominal segment. The first mysis measures 3.47 mm in body length and is slender (Fig. 10A). The second mysis measures 3.80 mm in length and shows pleopod buds (Fig. 10B). The third mysis is longer measuring 4.36 mm in length, and has one tooth on the dorsal margin of the rostrum (Fig. 10C). Pleopods are two segmented.

*Trachypeneus* (Fig. 11). The mysis of this genus can be distinguished by the length of the rostrum, which just reaches the margin of the eyes. The fourth and fifth abdominal segments bear dorsal spines, of the former being the shorter of the two. The first mysis measures 2.80 mm in body length and

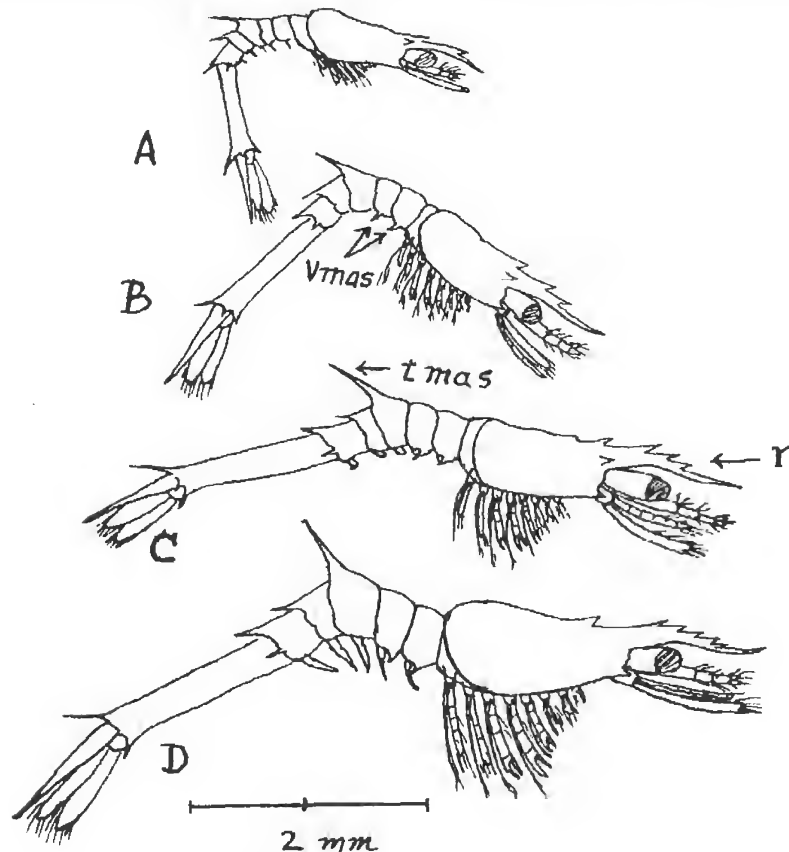


FIG. 12

is more transparent than the older larvae (Fig. 11A). The second mysis measures 3.62 mm in length and shows pleopod buds (Fig. 11B). The third mysis is not too transparent, measures 4.44 mm in length, and shows two segmented pleopods (Fig. 11C).

*Xiphopenaeus*. The mysis stages of this genus resemble the previous genus in measurements. The only difference is the lack of lateral spines on the fifth abdominal segment.

*Parapenaeus* (Figs. 12 & 13). These mysids are characterized by the rostrum extending beyond the eyes and a prominent spine on the third abdominal segment, followed by two shorter spines on the dorsal margins of fourth and fifth segments. The rostrum also bears teeth dorsally, and one tooth is added at each moult. The first mysis is slender, and measures 3.65 mm in length.

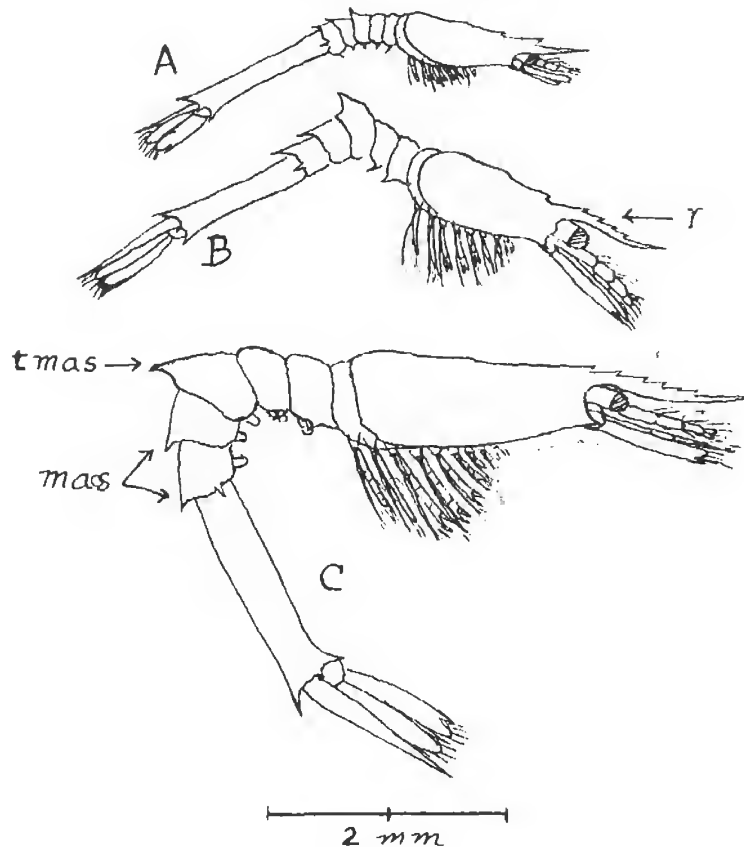


FIG. 13

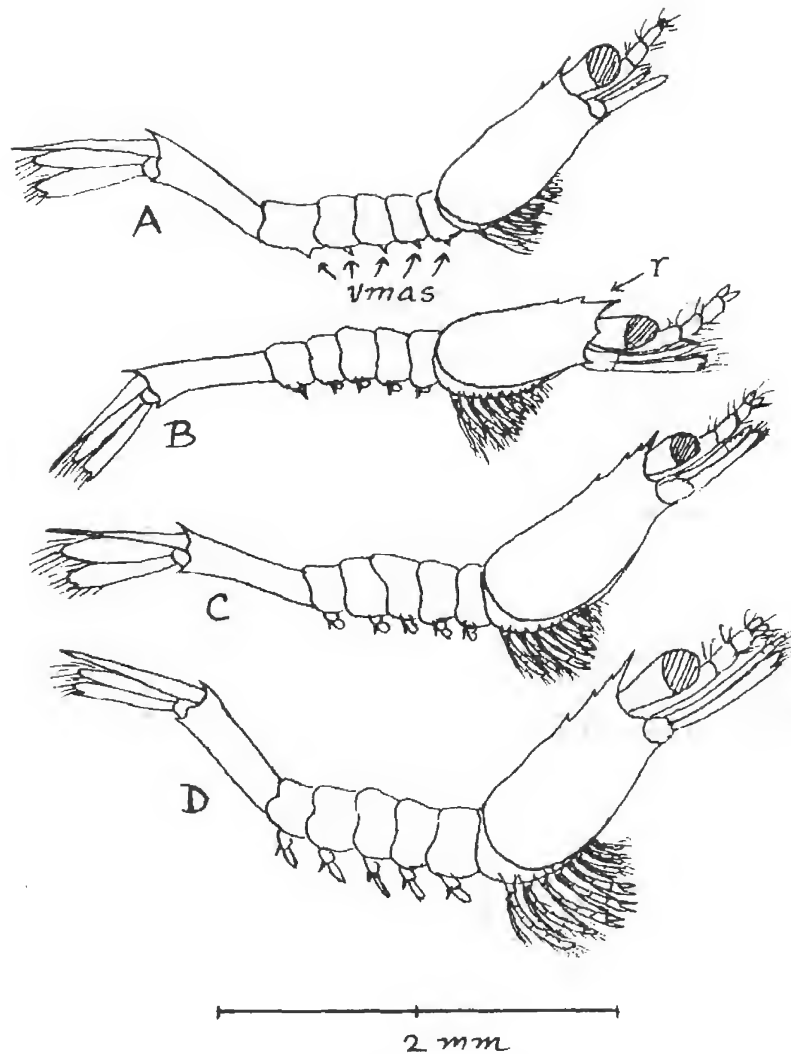
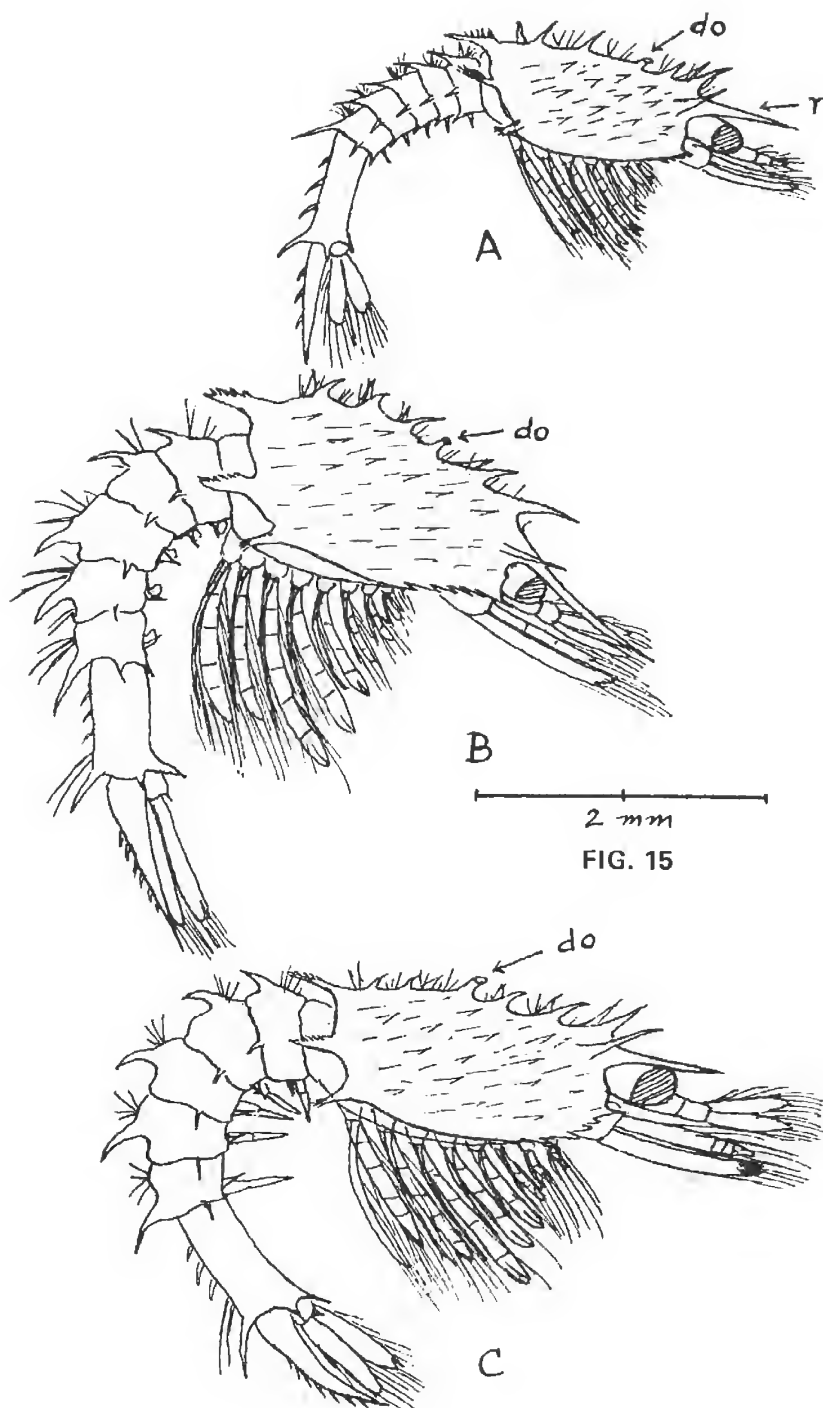


FIG. 14

The abdominal segments bear spines ventrally on the sternites of the first to fifth segments. The rostrum is decurved with two dorsal teeth (Fig. 12A). The second mysis measures 4.44 mm in length. The rostrum has three spines and the sternal spines on the third to fifth segments have disappeared (Fig. 12B). The third mysis measures 5.55 mm, has five rostral teeth, and two segmented pleopods (Fig. 12C). The characters of these larvae agree with those given by Pearson (*op. cit.*).



Along with these mysis stages, occasionally slightly different types of mysids were noticed (Fig. 13). They were generally larger and, while sharing the generic characters of the mysis described above, they have a longer rostrum with more teeth. The dorsal spine on the third abdominal segment is triangular, being broad at the base. The two short dorsal spines on the fourth and fifth segments are present. The first mysis measures 3.96 mm, the second 5.28 mm and the third mysis 8.00 mm in body length. It is obvious that these mysids are larger than those of *P. longirostris*. The rostral teeth numbered one for the first mysis, four for the second, and six for the third mysis (Fig. 13A, B, C). The fourth mysis was never caught.

*Sicyonia* (Fig. 14). The mysis is characterized by a short rostrum (shorter than the eye), absence of dorsal spines on the abdominal segments, and presence of ventro-median spines on all the five abdominal segments. The larvae are also more robust. The first mysis measures 2.45 mm (Fig. 14A) and shows the ventro-median spines clearly. The second mysis measures 2.90 mm and shows rudiments of pleopod buds (Fig. 14B). The third mysis measures 3.20 mm in length, and shows small two-segmented pleopods (Fig. 14C). The fourth mysis measures 3.35 mm in length and shows prominent and two-segmented pleopods. The features of these larvae are in general agreement with those given by Cook and Murphy (1965).

*Solenocera* (Fig. 15). The mysids are the easiest to be identified by the spiny nature of the whole body. The rostrum is long, and the carapace as well as the abdomen carry long spines. The dorsal organ is the salient feature of *Solenocera* mysis, the function of which is disputed. The first mysis measures 4.42 mm in length and bears ventro-median spines (Fig. 15A). The second mysis measures 6.85 mm in length and bears strong spines dorsally on the abdominal segments. The pleopods are beginning to show (Fig. 15B). The third mysis measures 6.95 mm in body length, and bears dorsal abdominal spines and two-segmented pleopods (Fig. 15C). These larvae were particularly abundant in waters deeper than 54 meters.

#### Postlarvae

Postlarvae of *Penaeus*, *Parapenaeus*, *Trachypenaeus*, *Sicyonia*, and *Solenocera* were collected during the present study. Only the postlarvae of *Penaeus* and *Trachypenaeus* are described here. These were most commonly taken in the plankton.

*Penaeus* (Fig. 16). The postlarvae are distinguished by long and slender bodies, thin rostrum, and long sixth abdominal segment. The post-larvae were identified with the aid of the key worked out by Williams (1959). In Figure 16, the first and the third postlarvae of *Penaeus fluviatilis* are given. The first postlarva is slender, and measures 4.5 mm in body length. The ros-

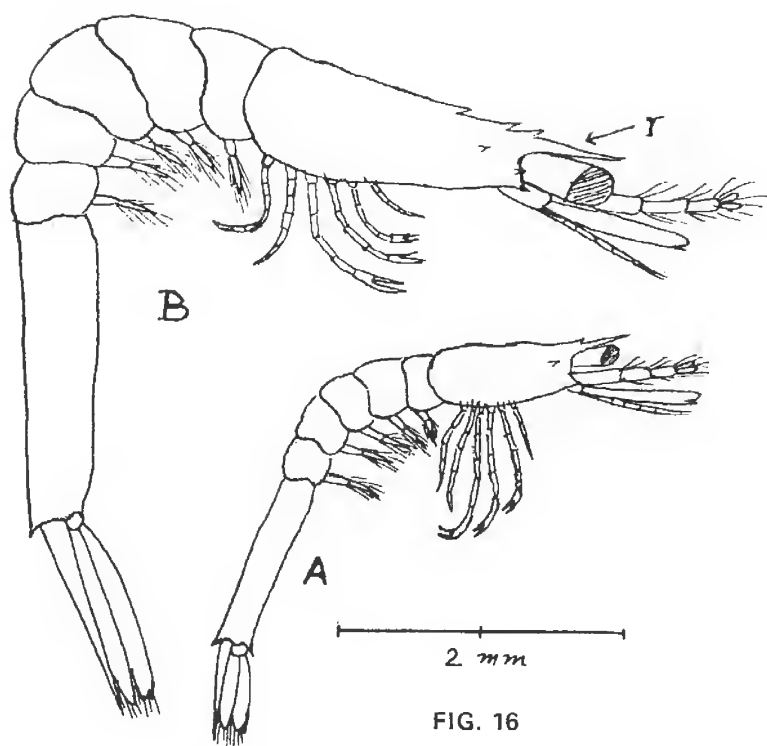


FIG. 16

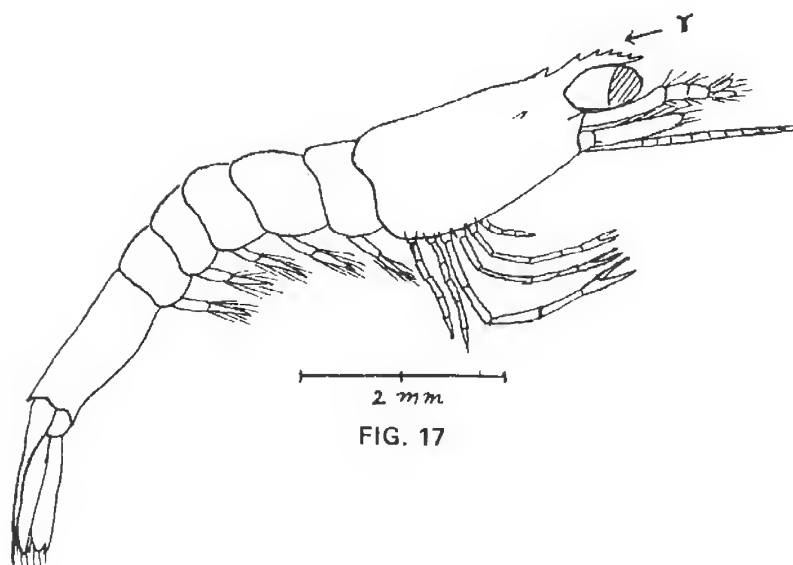


FIG. 17

trum evens with the margin of the eye, and bears one dorsal tooth (Fig. 16A). The third postlarva measures 8.38 mm in length and has three rostral teeth. The rostrum just reaches the margin of the eye (Fig. 16B). Though the postlarvae of brown shrimp were taken, they are not described here. Pink shrimp postlarvae were least abundant of the three species.

*Trachypeneus* (Fig. 17). The postlarva is thick and the sixth abdominal segment is not as long as in *Penaeus*. The rostrum does not reach up to the margin of the eye, and it bears seven dorsal teeth. It measures 8.45 mm in body length, and judging from its size and the number of rostral teeth it is the fourth postlarval stage. Younger postlarvae were not common in the plankton samples.

#### REMARKS

The diagnostic characters of different larval stages of various species of the six genera have been pointed out to facilitate easier identification. Plankton samples collected from any level of a water column (of the area sampled) and from any depth invariably contain a mixture of stages and species, and it is possible to identify these larvae with the help of the drawings presented as far as the Gulf of Mexico genera are concerned. It appears to be a general feature with crustaceans that their larval stages occur together in any area. The proportions of stages and species, however, exhibit seasonal variations. This has been observed by Gurney (1924, 1942), Pearson (1939), and Eldred *et al.* (1965). Gurney (1924) remarks that crustacean larvae have the power of keeping together or collecting at a suitable locality and may not be at the mercy of the currents as much as it is generally supposed. The correspondence between the bathymetric distribution of the larval species and the adults appears to lend support to this surmise.

It has been found that the identical stages of any species are not uniform in size, and identification based on the size alone is liable to be misleading. That within an instar the body size of the larvae may differ has been pointed out by Hudinaga (1942) and again by Renfro and Cook (1963). Though growth has been known to occur only at each molting in crustaceans it is interesting that size differences within an instar are noticeable.

It is difficult to separate the three species of *Penaeus*, *P. fluviatilis*, *P. aztecus*, and *P. duorarum*, based on larval morphology or morphometry. The white shrimp and the pink shrimp are relatively shallow water species and the brown shrimp is known to occur in deeper waters (Burkenroad 1939). Therefore, the larvae caught in deeper waters may belong to the brown shrimp, and those in shallower waters may belong to



either white or pink shrimp, depending on the geographical locality. However, this is complicated by the offshore movements of all the species into deeper waters with the temperature decline as has been shown in the case of *P. fluvialis* (Weymouth, Lindner and Anderson 1933). The eggs of *Penaeus* can be distinguished by the narrow perivitelline space.

The two common species of *Trachypeneus* in the Gulf of Mexico are *T. similis* and *T. constrictus*, and their ranges overlap (Burkenroad 1939). No descriptions of the larvae of *T. similis* are available, and it is hard to distinguish the larvae of these two species. Similarly, the protozoa of *Xiphopeneus* resembles *Trachypeneus* but for one small seta on the second endopod and many times this is lost, making it difficult to separate the protozoae of the two genera. The mysis of *Trachypeneus* can be easily identified by the lateral spines on the fifth segment, though Cook (1966) says that the rostrum can be used for this purpose. However rostral length, in my experience, is not a dependable character. Pearson (1939) described only two mysis stages of *T. constrictus* and his second mysis appears to be the third mysis because of two segmented pleopods. Also, the lack of lateral spines on the fifth abdominal segment casts a doubt that his larvae could belong to *Xiphopeneus*. Unfortunately, there is no information on the development of other *Trachypeneus* species since Pearson's work.

The present larvae of *Parapenaeus* agree with the descriptions of Pearson (1939) and Heldt (1938). It has been noticed that the mysis stages may differ slightly in morphology within the species. The dorsal spine on the third abdominal segment looks different in some larvae as well as the rostral length and shape (Figs. 12 and 13). This has been pointed out earlier by Heldt (1938). The most common species in the Gulf of Mexico is *P. longirostris* (Williams 1965). *P. americanus* is relatively a deep water species (Springer and Bullis 1956).

Both *Sicyonia dorsalis* and *S. brevirostris* occur in depths from inshore to the continental shelf (Williams 1965). *S. stimpsoni* is a shallow water species confined to the inside of 90 m contour (Lunz 1957). During the present investigation *S. dorsalis* was most commonly taken. The larval stages of *S. brevirostris*, *S. stimpsoni*, and *S. wheeleri* have been described and it is possible to distinguish these species based on the lateral setal formulae (Cook and Murphy 1965). Again, the short seta on the endopod is often lost, and the present larvae could belong to *S. brevirostris* (1 + 2 + 3) or *S. dorsalis* (1 + 2 + 2). The life history of *S. dorsalis* has not been described.

The three species of *Solenocera* known to occur in the Gulf of Mexico are *S. vioscai*, *S. atlantidis*, and *S. necopina*. These species inhabit waters 18 to 329 m deep and *S. necopina* occurs

in shallow waters as well (Williams 1965). The mysis can be distinguished from the sergestid mysis by the presence of the dorsal organ. The different species are identified based on the length and shape of the rostrum and the structure of the spines on the carapace (Heegaard 1966). There is practically no information on the *Solenocera* from the Gulf of Mexico. The most common species on the Louisiana and Mississippi coasts is *S. vioscai* (Burkenroad 1936), and the present larvae could belong to this species.

The significant point during the present investigation has been the correspondence between the bathymetric distribution of the larval genera and the known ranges of the species of the six genera. *Penaeus* larvae were obtained in depths from 10 to 90 m, *Trachypeneus* larvae mostly from 10 to 54 m, *Xiphopenaeus* larvae from 10 to 90 m, *Parapenaeus* larvae mostly from 36 to 90 m, *Sicyonia* larvae from 10 to 72 m mostly, and *Solenocera* larvae from 18 to 90 m. The adult ranges are: Pink shrimp 0-109 m, white shrimp 0-78 m, brown shrimp 0-180 m; *P. longirostris* 25-145 m; *T. constrictus* 20-37 m; *T. similis* 5-55 m; *X. kroyeri* 5-36 m; *S. dorsalis* 5-85 m; *S. brevirostris* 5-85 m; *S. vioscai* 36-72 m; *S. atlantidis* 18-329 m; and *S. necopina* 5-183 m; (Burkenroad 1936, 1939 and Williams 1965). From regular observations on the distribution and seasonal abundance of these larvae, it has been possible to gain an understanding of the breeding areas of the species belonging to the six genera. The life histories of species of *Trachypeneus*, *Xiphopenaeus*, and *Solenocera* need to be worked out. It is a matter of conjecture whether the larvae of the species of one genus (except *Sicyonia*) can be distinguished by morphological characters alone, or whether one has to investigate at the biochemical or molecular level.

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# Gulf Research Reports

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Volume 3 | Issue 2

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January 1971

Discovery of the Carolina Marsh Clam, *Polymesoda caroliniana* (Bosc), A Supposed Florida Disjunct Species, in Everglades National Park, Florida

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DOI: 10.18785/grr.0302.08

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DISCOVERY OF THE CAROLINA MARSH CLAM,  
*POLYMESODA CAROLINIANA* (BOSC), A SUPPOSED  
FLORIDA DISJUNCT SPECIES, IN EVERGLADES  
NATIONAL PARK, FLORIDA<sup>1</sup>

by

D. C. Tabb and D. R. Moore

INTRODUCTION

The presence of disjunct species of animals on either side of the Florida peninsula has been reported by a number of authors. The littorinid mollusk, *Littorina irrorata* Say, which has a range from Massachusetts to the Rio Grande of Texas, except for south Florida, is one such species (Requaert 1943). The marsh crab, *Sesarma cinereum* (Bosc), is another example of an animal with a distribution from Virginia to the western Gulf of Campeche except for a break in southern Florida (Rathbun, 1918). Williams (1965) lists 23 species of crustaceans having interrupted distribution at the Florida peninsula. This report on discovery of a breeding population of the Carolina marsh clam, *Polymesoda caroliniana* (Bosc) in southern Florida supports the contention by Hedgpeth (1953) that at least some, perhaps many, of the disjunct records may be a result of insufficient collecting in south Florida. The Carolina marsh clam has been assumed to be a typical disjunct species since it was described as such by van der Schalie (1933). It was not included in Marine Shells of Southwest Florida by Perry (1940) nor in Florida Marine Shells by Vilas and Vilas (1945). Abbott (1954) apparently knew of no southern Florida material, and recent examination of collections of this species in the U. S. National Museum provided no material south of New Smyrna on the east coast or Fort Myers on the west coast of Florida. Gunter and Hall (1963) found a breeding colony in the St. Lucie River estuary near Fort Pierce, Florida extending the range nearly 275 km farther south along the Florida east coast but gave no details on the size of the population.

The initial discovery of a single valve of the Carolina marsh clam in extreme southern Florida was made by Tabb and Manning (1961) in deltaic muds at the mouth of the East River where it enters Whitewater Bay in Everglades National Park. Since 1962 sufficient discoveries have been made in Everglades National Park to prove the existence of a breeding population occupying two rather different but adjoining habitats over an extensive area of southern coastal marsh (Figure 1).

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Contribution #1395 from the University of Miami, Rosenstiel School of Marine and Atmospheric Science, Miami, Florida.

## SYNONYMY AND DIAGNOSIS

When the first specimen was found in Everglades National Park it was necessary to consult several old publications for a description, and to unravel the synonymy. Because of the general scarcity of these publications and relative rarity of the species it is thought desirable to reproduce the most important of these references.

Dr. H. A. Rehder, Research Curator of Mollusks, U. S. National Museum, has kindly made the following comments concerning the nomenclature: "*Polymesoda* was used as a generic name by von Martens, *Biologia Centrali Americana*, Moll., p. 540, 1900, and usually by others who worked with it since 1900. I think the group is generically distinct from the Old World cyrenas. However, the fact is that *Cyrena* will go out, its type being a *Corbicula*, and the Old World group will be called *Geloina* Gray."

Diagnosis of Family *Cyrenidae* (= *Corbiculidae*) after Dall, Wm. H., 1895.

- p. 540. Anatomy as in *Veniellinae*, except that the mantle is more open ventrally, the siphons distinctly developed, short, united more or less, usually with papillose orifices; dioecious; fluviatile or estuarine.

Shell porcellanous, with a conspicuous epidermis, usually with concentric sculpture; valves equal, free, closed, usually with plain margins; area obscure or none; ligament and resilium external, paravincular, opisthodetic; adductor scars subequal, separate from the pedal; pallial line simple or with a small sinus; hinge with anterior and posterior laminae usually double in the right, single in the left valve, distinctly separated from the cardinals; cardinal teeth bifid at the summit, three in each valve when none are obsolete.

Lias to Recent fauna.

Synonymy after Dall, Wm. H., 1903.

- p. 1447. *Cyrena* (*Polymesoda*) *caroliniana* (Bosc)  
*Cyclas caroliniana* Bosc, Hist. Nat. des Coq., iii., p. 37, pl. xviii., fig. 4, 1802; Say, Am. Conch., vii., lxii., 1833.

*Cyrena caroliniensis* Lamarck, An. s. Vert., v., p. 553.

*Cyrena carolinensis* Hanley, Rec. Shells, p. 93, pl. xiv., fig. 54, 1842.

*Cyrena caroliniensis* Holmes, Post-Pl. Fos. S. Car., p. 31, pl. vi., fig. 7, 1860.

*Cyrena floridana* Sowerby, Conch. Icon., 1878; not of Conrad, 1846.

Pleistocene of Simmons Bluff, South Carolina, and of North Creek near Osprey, on the west coast of Florida; Recent from South Carolina to Florida and westward to the coast of Texas, in streams and brackish water near the sea.

Synonymy after van der Schalie, H., 1933.

*Cyclas caroliniana* Bosc, 1802, Hist. Nat. Coq., 37, pl. xviii, fig. 4; Chenu, 1845, Biblio. Conch., 3: 27; Dall, 1903, Proc. Biol. Soc. Wash., 16: 6; Walker, 1918, Syn. Fresh-Water Moll. N.A.: 85.

*Cyrena caroliniensis* Bosc., Dall, 1903, Trans. Wag. Free Inst. Sci., 3: 1447.

*Cyrena caroliniensis* Lamarck, 1818, Hist. Nat. des An. sans Vert., Part ii, 568; Dubois, 1825, Ep. Lam. Test.: 65; Ravenel, 1834, Cat. Rec. Shells: 4; Conrad, 1853, Proc. Acad. Nat. Sci. Phila., 6: 246; Prime, 1865, Smith, Misc. Coll. 145: 11; Paetel, 1890, Cat. Conch. Samm., (4th Ed.), 3: 97.

*Cyrena carolinensis* Bosc, Say, 1819, Nich. Encycl., (3rd Ed.), 4: 56; Hanley, 1842, Rec. Shells, p. 93, pl. xiv, fig. 54; DeKay, 1843, Zool. New York, V: 226, pl. xxv, fig. 266; Wheatley, 1845, Cat. Shells U. S., p. 6; Conrad, 1846, Am. Jour. Sci., 2: 394; Gibbes, 1848, Appen. Geol. S. C., p. xxi; Philippi, 1849, Abild. und Beschreib. Conch., p. 8, pl. ii, fig. 4; Deshayes, 1854, Brit. Mus. Conch. II; Say, 1858, Conch. U. S., p. 56, 226; Dall, 1889, Bull. U. S. Nat. Mus. 37: 56; Simpson, 1889 Naut., 3: 80; Johnson, 1890, Natur., 4: 4; Baker, F. C., 1891, Proc. Acad. Nat. Sci. Phila.: 45; Simpson, 1892, Naut., 6: 40; Hinkley, 1907, Naut., 21: 80; Mazyck, 1913, Cat. Moll. S. C.: 25; Johnson, 1919, Naut., 33: 7.

*Cyrena caroliniensis* Bosc, Stark, 1828, Elements Nat. Hist., 2: 100; Hanley, 1842-56,

Descrip. Cat.: 93; Holmes, 1860, Post-Pl. Fos.  
So. Car.: 31, pl. vi, fig. 7; Fischer, 1887, Man.  
de Conch.: 1091.

*Unio carolinianus* Bosc, Ferussac, 1835, Mag.  
de Zool., No's. 59, 60, V:26; Conrad, 1853,  
Proc. Acad. Nat. Sci. Phila., 6:246.

*Cyrena carolinensis* Say, Roemer, 1849, Mol-  
lusca: 453.

*Cyrena carolinensis* Lamarck, Nylander, 1921,  
Naut., 34: 120.

#### DISCUSSION

Following the first discovery of *P. caroliniana* at the mouth  
of the East River in Everglades National Park (Tabb and Man-  
ning, *op. cit.*) no additional material was found there until the

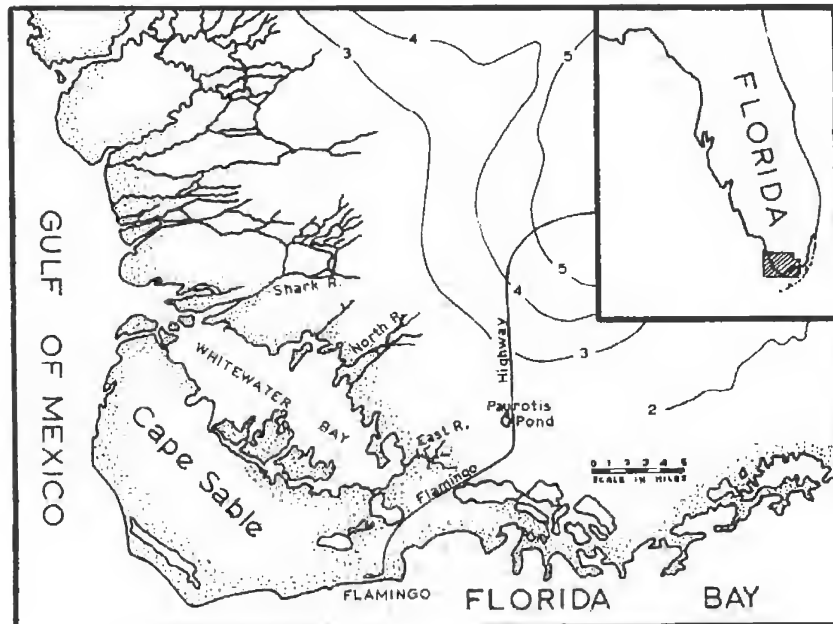


Figure 1. The Cape Sable region of South Florida  
showing Paurotis Pond and the North and  
East River systems where *Polymesoda car-  
oliniana* populations are known to occur.



period of 4-23 March 1962 when large numbers of moribund specimens were found being washed ashore at Paurotis Pond, a fresh-water lake about 12 miles north of Flamingo on Florida Highway 27 (Figure 1).

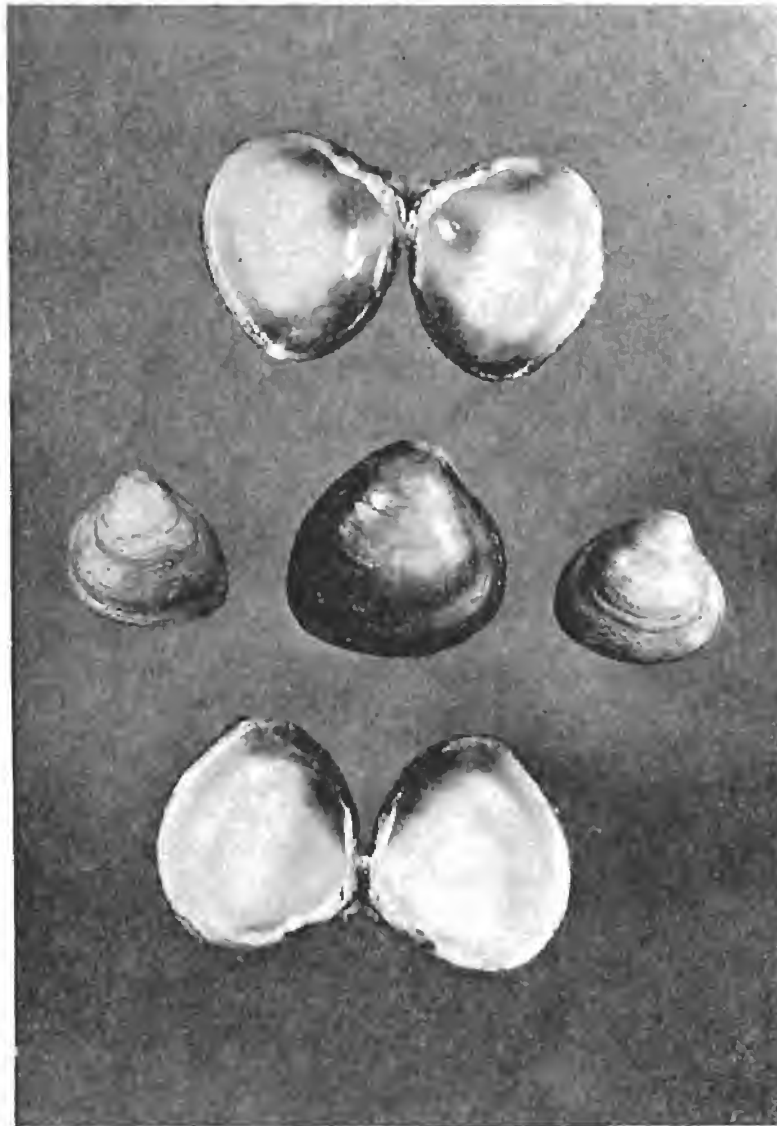


Figure 2. External and internal aspect of shells of *Polymesoda caroliniana* from Paurotis Pond showing thick, highly colored valves with flaky periostracum.

The abnormal condition under which the specimens were collected was a result of a severe, prolonged invasion of wind-driven salt water from Whitewater Bay during a southerly windstorm on March 4 through 10 (Craighead and Holden 1965). This saline invasion occurred at the peak of a severe drought which had lowered the levels of fresh water in the coastal region surrounding Paurotis Pond thus paving the way for replacement by wind-driven salt-water. During the saline intrusion the salinity increased from 2 ppt to 20 ppt in six days.

Many hundreds of the clams, all near the 40.0 mm maximum size for the species given by Abbott (*op. cit.*) were washed ashore by the strong winds which caused the saltwater invasion. After stranding they were killed by the heat of the sun and then preyed upon by crows, racoons and seagulls from nearby Florida Bay. Although the mortality of *P. caroliniana* from these causes was extensive it was apparently not total, because a visit to the pond on the following May 4 produced a small sample of living adults. At that time the salinity had fallen to about 12 ppt. The survivors were located in 0.5 to 0.8 m of water in soft, fine-grained calcium carbonate mud having the local name of Flamingo marl.

Until August 1965, the Paurotis Pond population was the only known concentration of this species in the Park. However, during August and September 1965, and again in March 1966, additional specimens were found in headwater marshes of the North River some 13 km west of Paurotis Pond and about 5 km inland from the northern edge of Whitewater Bay.

#### HABITAT

*P. caroliniana* of Everglades National Park occurs in soft mud, generally 2.5 to 5.0 cm below the surface film of benthic algae and organic debris. All living specimens found by us have been in water less than 1 m deep although dead shell can be found on the bottom of the North River in 1 to 2 m depths.

The Paurotis Pond population occurs most abundantly in marginal shallows where the fresh-water needle rush, *Eleocharis cellulosa* Torr. is abundant, and where the yellow-flowering bladderwort, *Utricularia lutea* Birdsey and the euryhaline green alga, *Batophora oerstedii* var. *occidentalis* (Harvey) Howe, occur side-by-side. The water in this area is characteristically clear and without color imparted by organic material. The clarity of the water, the characteristically high pH of 7.8 to 9.0, and the general absence of humus in the mud all combine to produce a brightly colored form of *P. caroliniana* (Figure 2) having a high gloss, straw-yellow flaky periostracum and no erosion of the shell at the umbo as reported by van der Schalie. In addition to the above characteristics the shells of the Paurotis Pond population are more massive than specimens from the North River population.



Figure 3. Comparison of external appearance of adult *Polymesoda caroliniana* from Paurotis Pond (upper) and North River (lower).



Figure 4. Single valves of *Polymesoda caroliniana* from North River peat marsh illustrating eroded condition of the shell material approximately 6 months after death of the animal. Note periostracum fragment still adhering to upper specimen.

In the North River the living clams were found in an environment like that described by van der Schalie in that they occur in the soft mangrove peat deposits along the edges of the brackish-water creeks. In the same region small specimens may also be collected at some distance back from the creek edges in seasonally flooded marshes where water depth fluctuations of 15 to 60 cm are common due to accumulation of fresh-water runoff during the rainy season.

All living specimens in the North River peat had eroded umbos, thinner chalky shells, thick, dark periostracum and somewhat longer and flatter shell profile (Figure 3). The peats are slightly acidic and the shells are quickly eroded by solution after death of the animal (Figure 4). The shells dissolve appreciably in 3 to 4 months when left in flooded mangrove leaf litter in the marsh shallows. Solution of the calcified shell material is often far advanced before the periostracum has decomposed.

The dominant emergent vegetation in the North River habitat is a mixture of black rush, *Juncus roemerianus* Scheele, and stunted red and white mangroves, *Rhizophorae mangle* L. and *Laguncularia racemosa* Gaertn.

Van der Schalie subjected *P. caroliniana* from Back Creek, a tributary of the Neuse River near Beaufort, North Carolina, to "normal sea water" for 2 weeks. After that period 9 of an original 14 animals used in the experiment were still alive but the "bodies of the surviving specimens were so emaciated that it was evident that they had suffered starvation". Considering that his 14 test animals were collected from waters having salinity of 18.63 ppt and placed in "normal sea water" which, presumably was at about 35.00 ppt it is likely that they were also seriously affected by salt. The mortality at Paurotis Pond in Everglades National Park was initiated by salt intrusion which finally led to stranding and predation. Considering the habitat salinity of the breeding populations in Everglades National Park it is likely that the normal salinity range will be about 0.5 to 10.0 ppt with occasional rises to 12.0 to 15.0 ppt. The limited observations we have on reproduction, as indicated by the presence of 2-5 mm young, suggest that this occurs at salinity under 5.0 ppt and probably is most successful in fresh water. Van der Schalie himself took them in fresh water and noted that "Mazyck (1913) reports the salinity probably does not exceed the 3.5 ppt salinity tolerated by wild rice of the region (Palmer 1949)."

Table 1 records the salinity, temperature, and dissolved oxygen conditions prevailing at one of the marsh stations in the North River where a large colony was found. Living animals were collected at that station until late March 1966, when salinity exceeded 15.0 ppt and water temperature rose to 24.5° C.

**Table 1:** Maximum, minimum and average salinity (ppt.), temperature (C°) and average dissolved oxygen values (ppm) for five day sampling periods in each month measured at North River Station 6, Everglades National Park.

	Salinity (ppt)			Temperature (C°)			Oxygen (ppm)
	Maxi- mum	Mini- mum	Aver- age	Maxi- mum	Mini- mum	Aver- age	
1965							
17-20 Aug	20.8	17.7	19.3	32.3	30.0	31.7	3.75
13-17 Sept	0.0	0.0	0.0	29.0	24.8	27.9	0.80
11-15 Oct	5.5	0.0	3.0	28.2	23.9	26.4	2.75
8-12 Nov	10.0	6.2	7.9	25.6	24.2	25.5	5.20
6-10 Dec	8.0	5.9	6.5	21.0	17.7	19.7	6.00
1966							
3-7 Jan	13.4	9.5	10.9	24.0	21.0	22.6	5.75
28 Feb	13.8	12.5	12.9	18.0	14.4	16.5	6.75
1-4 Mar	15.5	14.6	15.0	24.0	23.5	23.7	4.50
28 Mar*	23.4	21.0	22.5	24.8	21.0	24.5	5.40
25-29 Apr	26.5	22.0	24.6	25.3	23.0	25.2	4.40
23-7 May	25.0	20.0	22.4	31.5	28.5	30.0	3.80
20-24 June	0.0	0.0	0.0	32.8	29.0	30.5	2.05
18-22 July**	0.0	0.0	0.0	31.0	29.6	30.5	2.60
15-19 Aug	0.0	0.0	0.0	29.7	29.0	29.4	2.00

\*Point of apparent total mortality of population at station 6.

\*\*Reproduction indicated by presence of 4-7 mm young in sediments of channel edges.

Successful re-colonization of the station, as evidenced by 2.5 mm young, was observed during the following July after the marsh had been re-flooded by fresh water. Gunter and Hall (*op. cit.*) recorded salinity of 0.15 to 26.3 ppt where *P. Caroliniana* occurred in the St. Lucie River with the majority of young animals (6 to 18 mm) being found when salinity was below 1.0 ppt. In a later paper (Gunter and Hall 1965) they recorded 109 specimens in the Caloosahatchee Estuary of Florida at salinities ranging from 0.13 to 19.8 parts per thousand. The length range was 7-25 mm.

#### SIZE AT MATURITY

Abbott (*op. cit.*) gives the size of *P. caroliniana* as 25.5 to 38.0 mm in length and about as high. This is in general agreement with measurements of south Florida specimens. A series of 25 adults from Paurotis Pond ranged from 27.0 to 36.0 mm in length, averaging 31.8 mm. The range in height was 26.0 to 33.0 mm with an average of 29.7 mm.

Shells of the North River series were noticeably larger. The shell length range was 33.0 to 47.0 mm with an average for the series of 40.3 mm while the height range was between 30.0 and 38.0 mm with an average of 36.2 mm.

No growth estimates are possible at this time, but the ultimate size of the mature individuals suggests that conditions for growth are somewhat more favorable in the North River habitat than in Paurotis Pond. This might be expected since the North River population is most abundant along the edges of

marsh drainage channels where water movement, hence food availability, is most dependable. In Paurotis Pond, the water movement is caused almost exclusively by wind circulation.

### CONCLUSIONS

The Carolina marsh clam, *Polymesoda caroliniana* (Bosc), is not a Florida disjunct species, but instead it occupies a restricted habitat in coastal marshes where little collecting has been done until recently.

Before drainage of coastal marshes it is probable that the species distribution was continuous along the east Florida coast in the marsh belt adjacent to the coastal lagoons and estuaries. However, as these marshes were drained for development of cities, breaks were made in the distribution.

Thus, colonies probably exist today only in extensive remnants of the marshes which have nearly natural overland flow of fresh water emptying into coastal bays and estuaries, such as that found in Everglades National Park.

The optimum habitat in southern Florida is found in a narrow belt of shallow marshland where the mangrove forests intergrade with fresh-water flora of the interior. The normal depths of water there range between 0.25 and 1.0 m. The salinity range there is 0.0 to 10.00 ppt but may rise to 20.0 ppt or higher during drought or during wind-driven intrusions of sea water.

The adults at least can tolerate salinity as high as 26.3 ppt for short periods of time but become adversely affected when salinity rises above 18 to 20 ppt.

South Florida populations apparently spawn during the spring and early summer coincident with the onset of the rainy season.

Discovery of the population of marsh clams in Everglades National Park provides yet another important reason for preserving the traditional volume and seasonal pattern of overland flow of fresh water into coastal marshes there.

#### ACKNOWLEDGEMENTS

The investigations that produced the material described herein were carried on during the period 1957 through 1966. They were sponsored in turn by the Florida State Board of Conservation (1957-1960), the U. S. Public Health Service, Division of Water Supply and Pollution Control (Grant Number WP-00400-01, 02, 03) and the U. S. Department of the Interior, Office of River Basins (Grant Number 14-16-0004-56). We gratefully acknowledge this support.

Doctor Moore's research on unpublished material in the U. S. National Museum was supported by National Science Foundation Grant GB-5055. We are especially indebted to Dr. Harald A. Rehder, Research Curator of Mollusks, U. S. National Museum, for comments on the validity of the generic name *Polymesoda*.

We are also pleased to acknowledge the assistance of the Superintendents and staff of Everglades National Park who encouraged the research and provided vital logistical support.

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Figure 1



Figure 2



Figure 3



Figure 4





Figure 5

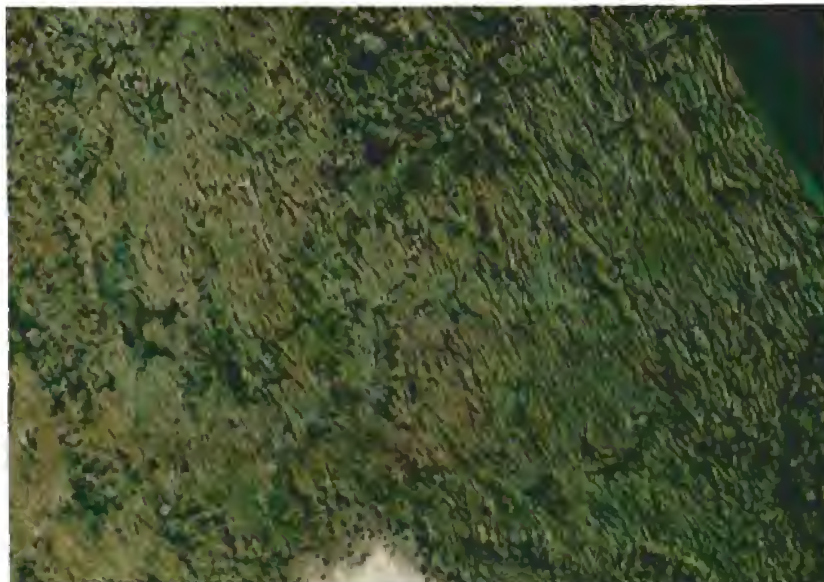


Figure 6

# Gulf Research Reports

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Volume 3 | Issue 2

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January 1971

Some Effects of Hurricanes on the Terrestrial Biota, With Special Reference to Camille

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DOI: 10.18785/grr.0302.09

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Gunter, G. and L. N. Eleuterius. 1971. Some Effects of Hurricanes on the Terrestrial Biota, With Special Reference to Camille. *Gulf Research Reports* 3 (2): 283-289.

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SOME EFFECTS OF HURRICANES ON THE  
TERRESTRIAL BIOTA, WITH SPECIAL REFERENCE  
TO CAMILLE

by

Gordon Gunter and Lionel N. Eleuterius

Gulf Coast Research Laboratory

Ocean Springs, Mississippi

INTRODUCTION

There have been very few articles concerning the effects of hurricanes upon marine and shore organisms. Some effects on fishes have been described by Hubbs (1962) and in that paper he reviewed some of the previous references.

Information on animals killed or injured by hurricanes is scarce because potential observers in areas where they strike are generally more concerned with practical personal matters than biological studies right after a bad storm. The senior author has been in or very close to seven West India hurricanes as they came ashore. Each time he was somewhat forewarned and had determined to make some type of quantitative appraisal of killed animals following these storms. However, on no occasion has this been done. Nevertheless, the two writers have collected some fragmentary information worth recording.

Some Damages to the Fauna on the Mississippi Coast

Hurricane Betsy—9-10 September 1965

When Betsy passed the Mississippi Coast on its way to devastating areas of New Orleans, the center was approximately 50 miles south of Horn Island. Thus the wind blew more or less from east to west along the Ocean Springs-Pascagoula coastal area. Following this storm hundreds of sea balls mostly of the marsh grass *Spartina* were found on the mainland beach of Mississippi Sound near Gulfport.

The water rose to a height of about six feet on the Laboratory grounds and left a strand of debris along the beach. In areas where there was marsh grass, thousands of little drowned mice, the Eastern Harvest Mouse, *Reithrodontomys humulis*, lined the shore in a little brown windrow which was sometimes 100 yards long without a break. Also lying on the beach every ten yards or so was a dead raccoon, *Procyon lotor*. There were so

many on the Laboratory grounds that they had to be hauled away. Raccoons are good swimmers and they certainly did not come from the surrounding nearby marshland. Horn Island, which lies eight miles offshore, was either completely or nearly submerged during this storm. The most reasonable assumption is that these coons were drowned in Mississippi Sound, after being washed off Horn Island and their bodies were finally blown onto the mainland shore.

#### Hurricane Camille—17-18 August 1969

This has been publicized variously as the worst storm that ever struck North America, or as the worst that has come ashore in this country in 143 years. Old, indefinite accounts indicate that something like this struck Florida in the 1700's. It is quite certain that Camille was the most powerful hurricane that has struck a well-populated shore of the United States. The weather planes flying through it clocked the winds at 218 mph and recorded the lowest natural barometric pressure that has ever been read (26.01 inches).

The "Big House," an old landmark of the Laboratory and of the coast, was splintered and even the brick pillars upon which it stood were washed away.

We have no way of quantifying the destruction of animals, except to say that the clean-up agency, the 43rd Battalion, Corps of Engineers, U. S. Army, reported removing 28 tons of animals from the beach between Biloxi and Gulfport on August 22-24. Most of these animals were dogs and cats, but some horses and cattle were mixed in. After the storm many dogs were homeless and many were systematically shot because they were starving.

Following the storm, the writer was waked up by a bird singing lustily just outside his window; this was the only bird seen for about a week. An unknown number of wild animals, birds, dogs and other life including human beings lost their lives in the storm; after about three days, the odor of decaying animals was noticed in the atmosphere and lasted about a week before it gradually went away.

The bird population and the squirrel population virtually disappeared but both came back after a few weeks time, most noticeably the jaybirds and a few gray squirrels (*Sciurus carolinensis*). The birds disappeared again, probably because they could find nothing to eat. This was certainly true of the squirrels and they were reduced to gnawing the bark off of felled water oaks (Gunter and Eleuterius 1971).

When the storm struck, the seeds of various nut trees—chiefly the hickory, black walnut, and thousands of pecans which



are planted in this area—were just beginning to mature. Many of these trees were blown down and approximately half of the foliage of those remaining was denuded by breakage of the limbs. The same thing was true of oaks and acorns. Additionally, the nuts themselves were beaten off of the trees that remained standing. Presumably for that reason the Eastern Gray Squirrel, which was quite common, had not returned in its former numbers by April 1970. Before the storm it was quite common to see as many as eight of these at one time in a relatively small area of trees in the senior author's front yard. After the storm, he saw none for one week and then he saw a lone squirrel. The squirrel population apparently increased in about three weeks to a month after the storm, then declined again. This observation would bear out the supposition that squirrels moving in from other areas could not find sufficient food and moved out again. The same thing apparently was true of the jaybirds.

There was a decided diminution in the number of birds which came to feeder stations during the following winter. For instance, dozens of birds and sometimes a few hundred in one afternoon formerly fed at a home facing the beach just to the side of the Laboratory grounds. The most numerous species, sometimes present in the dozens at a time, was the Savannah Sparrow. During the past winter only three or four have appeared at a time. The owner, before Camille, had to keep watch on the Starlings and jaybirds because they disturbed and ran off the others, but has had no trouble since the storm. General observations show that the Brown Thrashers, the jaybirds and the Cardinals are present in very diminished numbers even today (April 1970).

These facts have been noticed by other people and recorded, especially in *The Dixie Guide* by Mr. Clayton Rand who has gone through three bad hurricanes at his home in Gulfport. Mr. Rand has mentioned in his paper several times, the last being February and March 1970, that during former hurricanes there were many snakes and frogs everywhere in the area and that the mosquitoes were quite bad. He has remarked three times in his monthly newspaper that there was a great absence of life following Camille, even of the birds.

To the senior writer, however, the most amazing thing has been the disappearance of the ants up until this time (April 1970). The black carpenter ant and the Argentine fire ant and several other smaller species were quite common in his yard. Apparently they all succumbed to the storm, except for a minute yellow species that goes by the name of sugar ant, which has been seen one time. Bread and other foods set out for dogs and cats were formerly covered with ants in a matter of minutes; but, even this long after the storm, they may remain untouched by ants for days. We do not know the extent of destruction of the Argentine fire ant, but locally they are gone.

It is to be expected that termites and termite feeding animals and possibly woodpeckers would increase greatly in numbers due to the thousands and thousands of felled trees and rotting timber, a good bit of which, after having had the top broken off, is still upright.

#### Damages to the Flora on the Mississippi Coast

There are very few reports of the effects of hurricanes, typhoons, or cyclones (tornadoes) on coastal vegetation. Sauer (1962) reported the effects of cyclones on the coastal vegetation of a tropical island (Mauritius) in the Indian Ocean. Chamberlain (1959) and the U. S. Department of Agriculture (1960) reported some of the effects of Hurricane Audrey on the vegetation of south Louisiana. Previous hurricanes which struck the Mississippi coast inflicted minor damage to the vegetation; one of the worst of these storms known to the junior author occurred in 1947.

The "eye" or center of Hurricane Camille came ashore in the Pass Christian-Bay St. Louis area and the path was well marked by the effects of the storm on vegetation. The most apparent and obvious effect was the destruction of the trees. In Jackson County most of the trees blown down were oriented with the tops pointing toward the northwest. In Harrison County near Gulfport, the trees became oriented with the tops pointing toward the west-northwest and in the Pass Christian-Bay St. Louis area, they were oriented in an east-west direction, but some tree tops pointed eastward and some pointed to the west and the trees were nearly parallel in alignment (figs. 1 and 2). The paradoxical alignment was apparently a result of the initial winds from the east, followed after the "eye" passed over the area, by winds from the west. Trees west of Bay St. Louis near Pearl River were oriented with the tops toward the east-northeast and near Slidell, Louisiana, they were down in a north-east direction.

The intensity of winds from Hurricane Camille could be seen in the number of trees felled, the number increasing as the wind velocity increased toward the path of the "eye." In fact, without referring to other data, one could determine the storm's path by observing the east-west direction in which the trees were blown down and by the gradual increase in the numbers of trees destroyed as the center of the path was approached.

Tornadoes or extremely turbulent winds ripped through many areas on the periphery of the hurricane and the paths of their "touch downs" were well documented in the vegetation. In Magnolia State Park, which almost adjoins the Laboratory property, there is one area 50 feet wide and 17 tree lengths long, which the second author attributed to these tornadic gusts.

The junior author conducted two vegetational surveys to compare the intensity of damage to areas on the periphery of Hurricane Camille with areas nearer the center. In Jackson County, these surveys showed that in one tract, 4% of the trees were blown down and 10% were damaged to the point that survival was in question. The plant community was dominated by *Quercus nigra* (water oak) with *Pinus elliotii* (slash pine), *Carya glabra* (hickory) and *Quercus rubra* (red oak) being the subdominant species. This 40-acre tract in Magnolia State Park was approximately 22 feet above sea level. Destroyed trees in decreasing order were: red oak, slash pine, water oak, and hickory. It was noted that the heart wood (xylem) of the red oaks had been weakened by pathogenic attack and were rotted. Less than 10% of the pines destroyed were uprooted; they were twisted or broken off at heights ranging from 5 to 20 feet above the ground. The large tap-root characteristic of the pines apparently held the trees up; they were not blown down easily, but could be broken. Other trees blown down in adjacent plant communities were *Magnolia grandiflora* (Magnolia), (*Nyssa biflora* (black gum), *Liquidambar styraciflora* (sweet gum), and *Liriodendrum tulipera* (tulip tree or yellow poplar).

Another survey was conducted on 87 acres of forested land north of Pass Christian in Harrison County, bordering the Wolf River and Red Creek Road. Approximately 10 acres here were bottomland forest along the river and adjacent low-lying drainage areas. The rest of the land was approximately 25 feet above sea level and covered with *Pinus elliotii* (slash), *Pinus taeda* (loblolly) and *Pinus palustris* (longleaf) in various stages of growth. The owner considered the area a game reserve and left it undisturbed. Results of a sample showed that approximately 70% of the bottomland species were blown down. The species were *Magnolia virginiana* (sweet bay), *Liquidambar styraciflora* (sweet gum), *Taxodium distichum* (bald cypress), *Acer rubrum* (red maple), and the area was dominated by *Quercus nigra* (water oak). Ninety per cent of the trees in the low-lying area had diameters greater than 24 inches at breast height and there were between 100 and 150 trees per acre. An estimated total of 201,000 board feet of hardwood timber was lost.

Approximately 10,000 slash, loblolly, and longleaf pine trees with diameters greater than 10 inches were present on the higher sites and there were only 300 of these trees that were not damaged, i.e. 97% were destroyed. Many of those standing were not expected to survive due to lack of limbs, missing tops or split trunks. A total of 607,600 board feet of pine was estimated as lost. Many young trees were crushed by the falling trees, and other understory plants and habitats for wildlife were destroyed. At the time of the survey (March 1970), beetles, especially *Ips avulsus*, *Ips grandicollis*, and *Ips calligraphus*, had infested many of the downed trees and rot

had begun. The specific names of the beetles were furnished by Dr. Virgil Smith, entomologist, U. S. Forest Service, Gulfport, Mississippi. Twisted and split saw logs could not be salvaged for use. Paper wood operations were expected to be hindered by the tangled mass of trees. Practically all of the pine trees were second growth and ranged from 16 to 68 years old. The water oaks and other hardwoods were much older, ranging from 100 to 125 years.

These two tracts simply show by comparison that the most damage to the vegetation was caused by winds occurring near the center of Hurricane Camille's path.

Another observation was the destruction of *Quercus virginiana* (live oak) along the beach front from Biloxi to Pass Christian. Approximately 25,000 live oaks were growing along the beach before Camille and one-fourth were destroyed by wind and water and one-half were damaged. Those trees nearest the beach were partially inundated and the roots eroded by wave action. The immediate beating action of the wind and the physiological "drought" resulting from the salt spray reduced these evergreens to bare branches (figs. 3 and 4).

Many slash and longleaf pines may have been killed as a result of the inundation of low-lying areas near the mouth of the Wolf and Jourdan Rivers. The trees are dead but standing; however, this could be the result of other, internal damage since many trees on the barrier islands were covered by salt water and survived. This observation needs further study.

The Corps of Engineers, U. S. Army, estimated that a total of 1.2 million board feet of saw timber and one million cords of pulpwood in Mississippi were lost. On the Mississippi Test Facility in Hancock County, an estimated 6,000 cords of pulpwood were damaged and only 60% of the downed trees could be salvaged for lumber. It has been reported that a total of 290 million cubic feet of pine alone was lost in South Mississippi (Van Hooser and Hedlund 1969).

The barrier islands presented a pattern of destruction similar to that on the mainland. Petit Bois Island was affected relatively little but there was a gradual increase in damage on the islands to the west. Horn Island was heavily eroded on the outside beaches. The marsh vegetation was pushed down and pressed to the soil surface by the water as it passed over the island (figs. 5 and 6). Ship Island was cut into three pieces and more than one-third of the vegetation, most of which was herbaceous, was removed. Cat Island was heavily damaged. Large oaks were uprooted by wave action and many pines were broken by the wind. Large sand dunes were leveled, the sand redistributed over much of the adjacent low-lying marsh. Tons of plant materials swept from the Louisiana marshes and the barrier islands were deposited on the mainland in large windrows.

Marshlands were affected insignificantly because the water covered them early in the hurricane and they were not exposed to the terrific beating of wind and wave that occurred later. *Spartina alterniflora* (smooth cord grass) flowered on schedule (September through November). Shrubs found along the periphery of marshes, where they formed thickets, acted as baffles and protected trees and, in some cases, homes. Many upland understory areas were denuded of herbaceous and woody shrubs where they were located near water.

The botanical regime of South Mississippi was disturbed by Hurricane Camille of August 1969, probably to a greater extent than by any other hurricane in the history of the Mississippi, and the greatest influence on the terrestrial vegetation was the destruction of the trees.

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# Gulf Research Reports

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Volume 3 | Issue 2

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January 1971

## The Relative Abundance and Distribution of Penaeid Shrimp Larvae Off the Mississippi Coast

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DOI: 10.18785/grr.0302.10

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THE RELATIVE ABUNDANCE AND DISTRIBUTION  
OF PENAEID SHRIMP LARVAE OFF THE  
MISSISSIPPI COAST

by

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INTRODUCTION

Penaeid shrimp go through a complicated metamorphic life cycle involving a change in their habitat during the course of development. Adults inhabit and spawn in highly saline offshore waters, the larvae are planktonic and the postlarvae migrate into low saline coastal bays for their survival and growth. Spawning cycles of several species in the Gulf of Mexico have been studied chiefly by collecting the mature adults. A considerable volume of work has been done on the biology of the postlarvae, but information on the planktonic larvae is scanty. Assessment of reproductive cycles of marine animals based on the larval abundance is one of the several methods employed by biologists (Giese 1959). This method is particularly applicable to animals such as penaeid shrimp, which are benthonic.

The literature on the development and various other aspects of the biology of the penaeid shrimp is becoming voluminous. Many investigations have considered the spawning seasons, especially of commercially important species. Since Müller (1864) showed that the penaeid egg hatches into a nauplius, a series of investigations have traced the development of several species, especially those by Gurney (1924, 1927, 1942, 1943), Hudinaga (1942), Menon (1951), Heldt (1938, 1954, 1955), Heegaard (1966) from various parts of the world; Pearson (1939), Heegaard (1953), Dobkin (1961), Renfro and Cook (1963), and Cook and Murphy (1965a), from the Gulf of Mexico. Cook (1966) worked out a generic key for the identification of larvae to the generic level.

The commercial importance of penaeid shrimp evoked a great interest in the study of their biology, and a considerable amount of information has accumulated as reviewed by Williams (1965) and Lindner and Cook (1967). A useful bibliography has been prepared by Chin and Allen (1959). The first to un-

derstand that the penaeid shrimp spawn in the littoral water was Viosca (1920) who stated that *Penaeus setiferus* (Linn.), a synonym of *P. fluviatilis* Say when applied to North American white shrimp, spawns in the Gulf, chiefly on the evidence that mature shrimp are found only in outside waters. The young are said to live in the plankton of the Gulf until a size of 1 $\frac{1}{4}$  inch<sup>1</sup> is reached. Now it has been well established that this generalization is true. However, the size at which the postlarvae enter the bays is 7 mm (Weymouth, Lindner, and Anderson 1933). Actually some postlarvae are 12 mm or slightly more at this stage. After spending a variable period in the plankton, larvae metamorphose into postlarvae and migrate into coastal inland waters. They grow very rapidly in the low saline environment. This was first discovered by Viosca (1920), and was rediscovered by Gunter (1950), after it was forgotten or ignored for 30 years. Gunter states that the young white shrimp grow 25 to 45 mm per month during warmer months. Williams (1955a) has confirmed this.

The most thoroughly investigated species is the white shrimp, *Penaeus fluviatilis* Say, which has been studied in detail by Weymouth *et al.* (1933), Pearson (1939), Anderson, King and Lindner (1949), Gunter (1950), Anderson (1955), Lindner and Anderson (1956), Christmas and Gunter (1967) and Lindner and Cook (1967). According to these authors, the white shrimp spawn mainly from spring through late fall with variable peaks in different geographical areas. The brown shrimp, *P. aztecus* Ives, is believed to spawn through an extended period with little variation along its range (Gunter 1950), Kutkuhn 1962, and Williams 1965). The peak spawning seasons of this species are March-April and September-October. The pink shrimp, *P. duorarum* Burkenroad, has been studied extensively on the Florida coast by Eldred *et al.* (1961, 1965), Idyll, Jones and Dimitriou (1962) and Iversen and Idyll (1960). It breeds from spring to late summer or late fall according to these authors, but Roessler, Jones and Munro (1967) believe that it spawns year round.

The other species have not received as much attention as the species of *Penaeus*. From the available information (Pearson 1939, and Eldred *et al.* 1965), it appears that *Trachypeneus* spp. breed from February to November; *Parapenaeus longirostris* (Lucas) from April to June or October; *Sicyonia* spp. from January to December with summer peaks; and *Solenocera* spp. from February to June or November. These conclusions have been based on studies made on the larvae or the adults at a particular depth or a few depths.

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<sup>1</sup>Editorial note. Viosca always maintained that his measurements were in cm and they were botched by printers.



Most of the species of penaeid shrimp in the Gulf of Mexico appear to breed when the temperature rises in spring and exhibit peaks in spring or summer and in fall. The paramount importance of temperature in controlling the breeding and distribution of marine animals has been emphasized by Orton (1920), Thorson (1946, 1950), Ekman (1953), Gunter (1957), Johnson (1957) and Radovich (1961). Orton's rule states that, "most marine animals under normal conditions begin to breed either at a definite temperature, which is a physiological constant for the species, or at a definite temperature change, namely, at either the maximum or the minimum temperature of the locality." Rising temperatures induce gonadal development in most temperate organisms, and actual spawning takes place when a certain temperature, which varies with different species, is reached (Gunter 1957).

While the occurrence of mature adults and of larvae sheds light on the reproductive cycles of shrimp, the abundance of postlarvae in the backwaters offers corroborative evidence. Contributions on this phase of the shrimp life history have been made by Williams (1955 a,b, 1959 and 1969), Gunter (1961 a,b), Renfro (1960, 1961), Loesch (1965), Christmas, Gunter and Musgrave (1966) and Baxter and Renfro (1967). These authors have discussed the incidence of postlarvae in the bays, which occur in two or three waves, and these waves of abundance correlate with the spawning seasons.

It can be seen that the important larval phase of the life cycle has not received much attention. The occurrence of larvae is a definite sign of spawning activity, especially of the benthonic animals or sessile animals such as oysters (Korringa 1957). The first study purely on larval distribution was made by Eldred *et al.* (1965) who discussed trends in abundance in west Florida waters up to 37.8 m deep, and showed that spawning peaks varied at different depths for various species of six genera. Temple and Fischer (1965) studied the vertical distribution of the four larval stages and elucidated their vertical stratification and diurnal changes. The same authors discussed the relative abundance and distribution of *Penaeus* larvae off Galveston (Temple and Fischer 1967), and showed that the breeding season tended to be more protracted progressively with depth, and that the peak spawning season differed at different depths.

Thus, the information on the distribution of larvae of various commercial penaeids of the South Atlantic and Gulf of Mexico is limited to these three studies. Sampling at one water depth and at one particular level in the water column will not yield accurate information on the previous spawning activity of benthonic animals. Also, the distribution of larvae in relation to season, temperature, salinity and depth is of fundamental biological interest.

The objectives of the present investigation are: (a) to delineate spawning seasons and the areas of as many species as possible based on larval abundance; (b) to study the spatial and seasonal distribution of penaeid larvae in relation to depth, temperature, salinity and seasons, which will indicate the movements of the spawners; (c) to inquire whether any correlation exists between occurrence of larvae and of adults in any area; (d) to examine the relationship between *Penaeus* postlarval abundance in the Mississippi Sound and larval and postlarval occurrence in the open sea; and (e) to study the vertical seasonal distribution of different stages, and to find out whether different developmental stages exhibit diurnal migrations.

Larvae of six genera, *Penaeus*, *Parapenaeus*, *Trachypeneus*, *Xiphopeneus*, *Sicyonia*, and *Solenocera*, were encountered and the information on these is presented here. Protozoal and mysis stages of *Gennadas* and *Artemisia* were collected, and these are new records from the Gulf of Mexico. They were reported by Subrahmanyam and Gunter (1970). The study was conducted from November 1966 to December 1968 inclusive.

## MATERIALS AND METHODS

Plankton samples were collected from three depths at six different stations in the Gulf of Mexico. Subject to weather conditions, cruises were made to all or some of the stations every month for the purpose of obtaining a night and a day series of samples.

### FIELD PROCEDURE

#### *Stations*

The sampling stations were established to provide 18 m depth intervals. Station I was of particular interest because of its location just off the western end of Horn Island, where the depth was 10 m. The exact locations of the different stations are indicated in Fig. 1 and Table 1. The R. V. *Gulf Researcher*, a 65-foot (19.8 m) boat owned by the Gulf Coast Research Laboratory was used for the sampling program.

#### *Equipment*

For salinity estimates water samples were collected with Nansen bottles from the two subsurface depths and with a bucket from the surface.

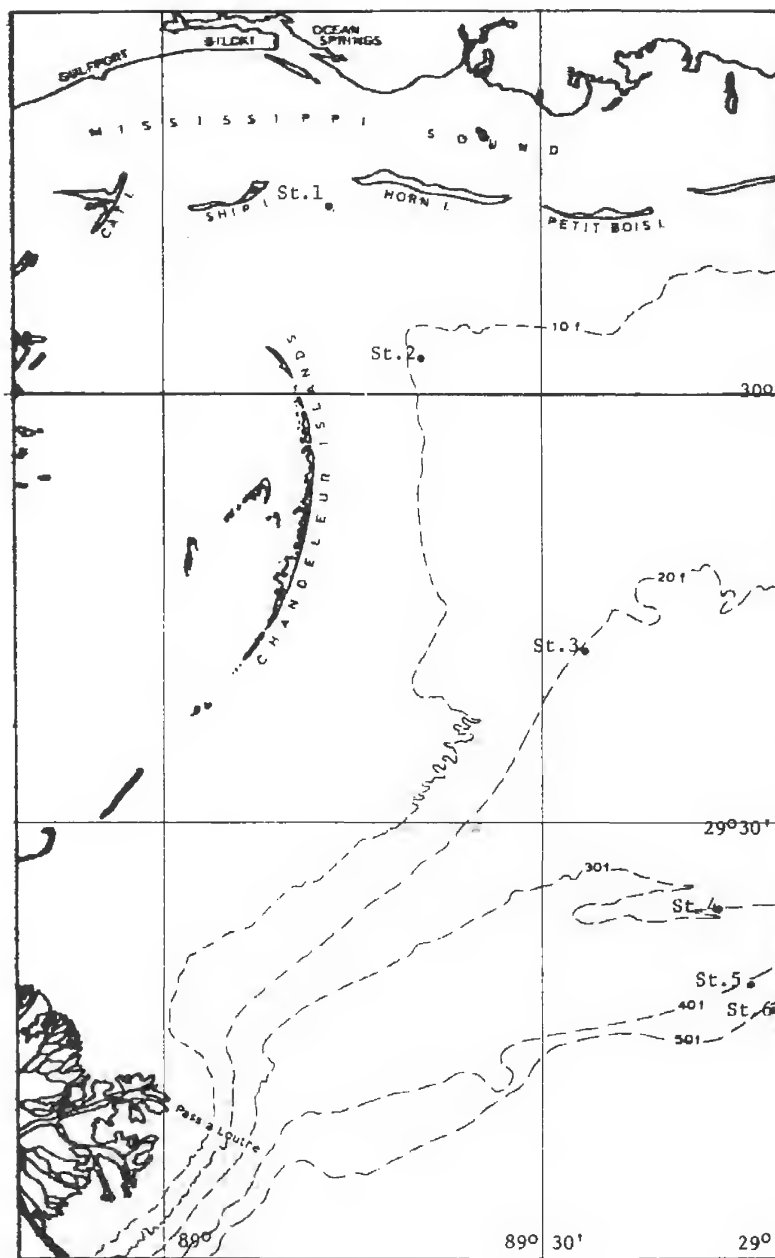


Figure 1. Station locations off the Mississippi Gulf Coast.

Table 1. Station locations and their depths

St. No.	Loran		Longitude West	Latitude North	Depth (m)
	3HI	3HO			
I	1108	3598	88°47'30"	30°13'15"	10.7
I	1110	3596	88°47'00"	30°12'30"	9.1
II	1220	3580	88°40'15"	30°02'30"	18.3
II	1220	3580	88°40'15"	30°02'30"	20.1
III	1440	3539	88°27'30"	29°42'00"	36.6
IV	1618	3494	88°17'00"	29°24'15"	54.9
V	1657	3480	88°14'00"	29°19'00"	73.1
VI	1683	3472	88°12'05"	29°17'15"	91.5
VI	1556	3457	88°31'00"	29°12'00"	109.8
VI	1562	3449	88°33'00"	29°12'00"	100.6

The positions of the stations were determined by Loran and the fathometer

NOTE: At times due to the drifting of the boat the Station locations differed slightly. Therefore, the altered positions for St. I, St. II and St. VI are also included in the Table.

Temperature profiles at each station were made with two bathythermographs, one that operated up to about 70 m depth, and the other up to about 275 m. Reversing thermometers mounted on the Nansen bottles offered a check on the bathythermograph temperature readings. Air temperatures were taken with a dry and wet bulb thermometer.

Plankton collections were made with three closing nets devised according to Hardy (1956). Each net measured 50 cm across the mouth, with a cross sectional area of 1964 cm<sup>2</sup>, and was 2 m long up to the bucket, including the canvas portion around which the belly rope for closing the net was looped. The netting was No. 3 Nylon with 0.33 mm mesh size. The surface net was towed from the stern of the boat. Simultaneously, the other two nets were towed at two subsurface levels. These two nets were fixed half the station depth apart (e.g., 9 m apart at 18.2 m station) on the same cable, with the bottom net attached 1 m above the sinker. Messengers for closing the nets were fixed on the closing devices. Three minutes were allowed for stabilization of the wire angle. Then the nets were towed at 600 rpm (3 to 5 km/hr) for exactly 20 minutes. At each station a circular course was taken to avoid drifting into deeper or shallower waters. The cable angle was measured at the beginning of each tow and attempts were made to keep the angle constant during the tow. Appropriate lengths of cable, read off a prepared chart, were let out for sampling at the desired depths (cable length = depth x cosecant of wire angle). Later the exact depths were calculated (depth = sine of wire angle x cable length). Since the position of the bottom net was known, and the length of cable sent out corresponded to the depth of the station, the bottom net was usually 1 m above the bottom. The

subsurface nets were always fixed with the same distance between them on the cable, and therefore the sampling depth of the middle net varied a little due to the different cable angles. After the tow was completed a messenger was sent down to close the subsurface nets. At the same time the surface net was hauled aboard. Plankton samples (from the three depths) were stored in separate bottles containing 10% formalin.

In my absence, sampling was done by trained personnel. The number of samples collected and the other details are given in Table 2.

Table 2. Details of the samples collected at 3 depths

TABLE 2. Location of water samples collected during 1966-1968					
Year & Month	Day St.	Number of samples collected		No. samples	Total
		No. samples	Night St.		
1966					
Nov.	II-VI	15	—	—	15
Dec	I-VI	18	—	—	18
				TOTAL	33
1967					
Jan	I-VI	18	I-VI	18	36
Feb	I-III	9	—	—	9
Mar	I-VI	18	II-III	6	24
Apr	I,II	5	—	—	5
May	I-VI	18	I-VI	18	36
June	I-VI	18	I-VI	18	36
July	I-VI	18	I-VI	18	36
Aug	I-VI	18	I-VI	18	36
Sep	I,II	6	I,II	6	12
Oct	I	3	II,III	6	9
Nov	I,II	6	III-V	9	15
Dec	I	3	I,II	6	9
				TOTAL	263
1968					
Jan	I-III	9	I-III	8	17
Feb	I	3	—	—	3
Mar	I-III,VI	11	IV-VI	8	19
Apr	I,II	6	—	—	6
May	I-IV	10	I-III	9	19
June	I, II, IV-VI	14	III	3	17
July	I-IV	12	I,II,V,VI	11	23
Aug	I-VI	18	—	—	18
Sep	I-III	9	III-VI	11	23
Oct	I-VI	18	I-VI	18	36
Nov	I-VI	18	I-VI	18	36
Dec	I-VI	18	I-VI	15	33
				TOTAL	248
GRAND TOTAL					544

Trawling was done with a 40-foot (12.19 m) balloon trawl with a mesh size of 3.2 cm from knot to knot. The boat speed was 1100 rpm (14 km/hr) for this purpose. The adult shrimp were picked out and preserved in 20% formalin for later identification.

#### LABORATORY PROCEDURE

Temperatures at different depths were read off the bathythermograms made at each station. Salinity was estimated with a Goldberg refractometer. The salinity at the depth where the middle net was calculated to be was read off the temperature-salinity curves drawn for each station by the procedure of McLellan (1965).

Plankton samples were allowed to settle for at least 48 hours and the settled volumes were recorded. All the penaeid eggs and larvae were picked out. The larvae were identified as to developmental stages and genera using Cook (1966) and other references. The larvae were stored in vials of 5% buffered formalin.

Since the numbers of larvae caught might be related to the amounts of plankton strained, correlation analysis was made between settled sample volumes and numbers of larvae per 500 ml standard volume. The nonsignificant correlation coefficients, 0.019 and 0.127, respectively, for day and night samples ruled out any such relationship. The numbers of larvae caught apparently depended on their general availability in the water column sampled. Hence the numbers of larvae per sample are compared in terms of catch per unit effort (20 min standard tow).

Adult shrimps were identified, measured, and sexed. Since the maturity condition reveals the breeding potential of the species, the different maturity stages of males and females were determined by methods set forth before (Subrahmanyam 1965b).

### RESULTS

#### HYDROGRAPHY

The two physical factors examined were temperature and salinity. The salinity ranges are given in Tables 3 and 4, and the temperature ranges in Tables 5 and 6.

##### *Salinity*

The minimum salinity during the study period was 18.5‰ at St. I and 26.8‰ at St. VI. But the maximum salinities varied between 36.6‰ and 38‰ only. The range of variation decreased seaward, the deeper waters tending to fluctuate over

**Table 3.** The ranges of salinity ( ‰ ) at different stations during 1966-1968.

St.	Depth	Minimum		Maximum		Range ‰
		Month	Sal. ‰	Month	Sal. ‰	
I	10	Jul. 68	18.5	May 68	36.6	18.1
II	18	Jul. 68	21.8	Nov. 68	37.1	15.3
III	36	Mar. 68	24.4	Oct. 67	37.7	13.3
IV	54	Oct. 68	27.2	Jun. 68	37.2	10.0
V	72	Aug. 68	26.0	Nov. 68	37.7	11.7
VI	90	Oct. 68	26.8	Aug. 67	38.0	11.2

**Table 4.** The ranges of salinity ( ‰ ) at different depths during 1966-1968.

St.	Surface			Middle			Bottom		
	Min.	Max.	Range	Min.	Max.	Range	Min.	Max.	Range
I	13.1	37.1	24.0	19.0	37.6	18.6	19.9	37.6	17.7
II	18.6	37.1	18.5	22.2	38.9	16.7	23.3	38.9	15.6
III	21.6	37.0	15.4	24.6	38.2	13.6	24.6	39.0	14.4
IV	16.8	36.8	20.0	25.0	38.0	13.0	28.8	38.9	10.1
V	18.6	37.4	18.8	25.6	38.0	12.4	24.9	38.0	13.1
VI	23.2	38.0	14.8	23.3	38.0	14.7	26.6	38.0	11.4
Range	10.1	1.2		6.6	1.3		8.9	1.3	

**Table 5.** Temperature ranges at different stations during 1966-1968.

St.	Depth (m)	Minimum		Maximum		Range °C
		Month	Temp. °C	Month	Temp. °C	
I	10	Jan. 67	12.3	June 68	30.1	17.8
II	18	Mar. 67	14.2	Aug. 68	29.4	15.2
III	36	Feb. 67	16.2	Aug. 68	30.1	13.9
IV	54	Jan. 68	16.9	June 68	28.5	11.6
V	72	Mar. 68	17.7	Oct. 68	26.4	8.7
VI	90	Mar. 68	17.4	Aug. 68	26.8	9.4

**Table 6.** Temperature ranges at different depths during 1966-1968.

St.	Surface			Midwater			Bottom		
	Min.	Max.	Range	Min.	Max.	Range	Min.	Max.	Range
I	12.2	30.4	18.2	12.2	31.0	18.8	12.5	29.5	17.0
II	13.6	30.1	16.5	14.4	28.0	13.6	14.4	29.0	14.6
III	13.6	30.8	17.2	16.1	31.5	15.4	16.4	29.0	12.6
IV	15.6	32.0	16.4	17.2	26.5	9.3	17.2	27.0	9.8
V	17.5	30.4	12.9	17.8	25.9	8.1	17.8	25.5	7.7
VI	17.8	30.4	12.6	17.2	28.0	10.8	17.2	21.9	4.7
Range	5.6	0.3		5.6	5.5		4.7	7.6	

a range of 11.2‰ as compared 18.1‰ at St. I. Months of low and high salinities differed among the stations (Table 3).

Surface, midwater, and bottom salinities at each station also showed certain trends. The minimum surface salinity ranged from 13.1‰ at St. I to 23.2‰ at St. VI. The midwater salinities fluctuated from 19.0‰ to 26.6‰. Minimum salinities were higher toward the bottom, and the range of variation decreased from 10.1‰ at the surface to 8.9‰ at the bottom. Maximum salinities at all depths of different stations varied only within 1.3‰ (Table 4).

No correlation was found between larval abundance and salinity, the correlation coefficients being 0.07 and 0.03, respectively, for day and night collections. In general, salinity fluctuations did not follow predictable patterns.

#### *Temperature*

Minimum temperature was recorded in winter in the inshore waters and at St. III and IV, and in spring at St. V and VI. When the average temperature is considered, inshore waters cooled down faster than the offshore waters. For deep waters 16.2 C was the lowest temperature recorded (Table 5). When the minimum temperature is considered, the St. VI minimum was 5.1 C higher than the St. I minimum. Maximum temperatures varied only over a range of 3.7 C. The range of fluctuations during the period of study decreased from 17.8 C at St. I to 9.4 C at St. VI. When the stations are compared (Table 6) it is seen that the minimum surface temperature was higher seaward, and the maximum temperature did not vary a great deal. Midwater and bottom minimum temperatures varied up to 4.0 C between St. I and III. At deeper stations variation was only in a range of 0.6 C. However, the range of fluctuations of maximum temperature was greater in midwater and bottom, 0.3 C, 5.6 C and 7.6 C at the surface, midwater and bottom respectively.

Vertical temperature profiles for all the stations are depicted in Fig. 2. Data are from the bathythermographs. In winter, isothermal conditions existed at St. II, IV and VI, and slightly warmer waters occurred toward the bottom of the other stations. In spring, temperature did not vary more than 0.6 C from surface to bottom at St. I, II, and III, while at St. IV and V considerable mixing of cold and warm waters was evident. Ninety meter waters (St. V) showed a gradual decrease in temperature toward bottom. In summer, typical thermoclines were found only at St. I and II. At all the other stations a gradual top to bottom decrease was evident. In fall, vertical mixing and isothermal conditions were evident at St. I through VI with some stratification at St. V and VI.



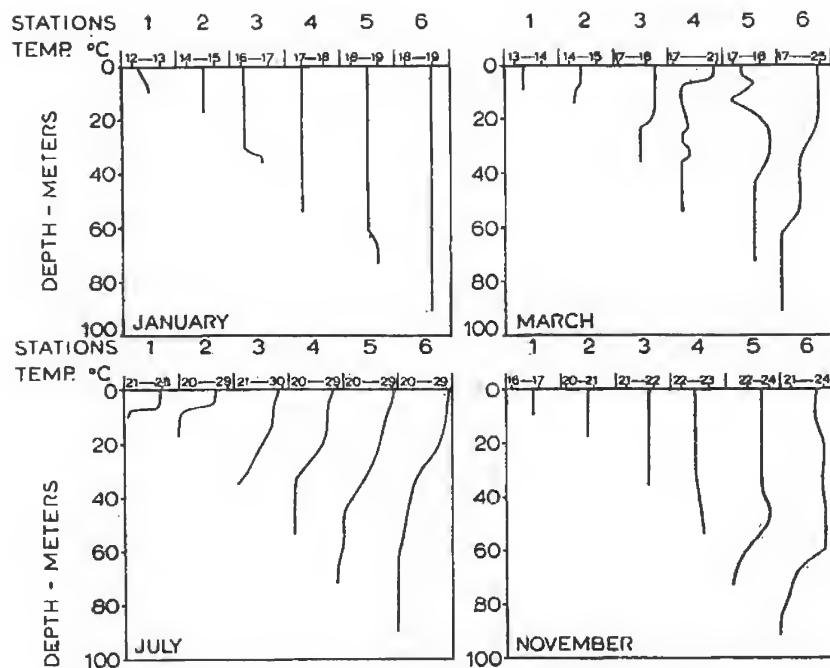


Figure 2. Bathythermograms for six stations in different seasons.

## SEASONAL ABUNDANCE AND HORIZONTAL DISTRIBUTION

### General

Larvae of the six genera, *Penaeus*, *Parapenaeus*, *Trachypeneus*, *Xiphopeneus*, *Solenocera* and *Sicyonia*, were caught in all depths at all the stations, but the relative abundance of in-

Table 7. Seasonal abundance of penaeid larvae expressed as average number of larvae per 20 min haul

Station	1967						1968					
	I	II	III	IV	V	VI	I	II	III	IV	V	VI
Spring	64	62	30	58	237	42	25	267	30	47	17	43
Summer	47	719	262	115	95	123	68	97	500	72	134	121
Fall	34	117	185	496	161	—	63	707	214	110	85	25
Winter	3	43	78	356	152	230	3	28	19	76	29	36
Average for two years 1967 - 1968.												
Spring	45	165	30	53	127	43						
Summer	57	408	371	94	114	122						
Fall	49	412	200	303	123	25						
Winter	3	36	49	216	91	133						

dividual genera varied in relation to seasons and depth. Average counts for each station and for the four seasons of 1967 through 1968 are given in Table 7.

Large numbers of larvae were taken in winter at stations beyond St. III, peaks being at 36 m depth in early winter and at 54 or 90 m depths in mid-winter.

In early spring the peak was still at St. IV, but by late spring the peak shifted to St. II. Fair numbers of larvae were caught at all stations during summer, indicating that penaeids were breeding over a wide area.

In fall, the peak was still at St. II but increased numbers were taken from deeper stations, for example at St. IV.

In winter, larvae were scarce at St. I to III and good numbers were taken at St. IV, V, and VI.

These trends in shifting of the larval peaks become clear if the average counts for the two years are examined (Table 7). Shrimp appeared to spawn in shallow or deep waters with warming or cooling of the environment. In spring spawning activity seemed to be concentrated at 18 m, in summer at 18 and 36 m, in fall at 54 m and in winter beyond 36 m. Minor spawning activity was evident at the other depths.

Correlation studies relating larval abundance and absolute *in situ* temperatures at various depths and stations failed to show any significant correlation, the correlation coefficients being 0.09 for day and 0.08 for night samples. This is to be expected in view of the fact that spawning activity heightens or even starts in spring in the inshore waters, when temperature starts rising, while in deeper waters it occurs all through the year. Table 8 indicates that shrimp in this area breed between average temperature range of 17 and 29 C. Within this range the spawning activity of the six genera, as indicated by the lar-

**Table 8.** Average seasonal temperatures (°C) at different stations during 1967-1968.

Station	1967						1968					
	I	II	III	IV	V	VI	I	II	III	IV	V	VI
Spring	21.4	19.5	20.1	20.7	20.4	20.6	22.2	20.8	19.6	20.1	18.0	19.3
Summer	25.3	23.3	24.1	23.9	22.4	22.6	29.5	28.2	28.4	25.7	24.9	24.6
Fall	23.2	23.3	22.6	21.3	21.6	—	21.0	23.8	24.5	22.9	23.2	22.7
Winter	14.6	15.8	16.9	18.3	19.3	19.1	13.9	16.0	17.1	19.6	21.9	21.6
For Two Years 1967 - 1968.												
Spring	21.8	20.2	19.9	20.4	19.2	19.9						
Summer	27.4	25.8	26.2	24.8	23.6	23.6						
Fall	22.1	23.6	23.6	22.1	22.4	22.7						
Winter	14.2	15.9	17.0	19.0	20.6	20.4						

val abundance, varies in such a manner that specific correlation with *in situ* temperatures may not show. In other words, larval abundance is not absolutely related to temperature changes between 17 and 29 C.

**Table 9.** Bottom temperatures (°C) at different stations in four seasons during 1967 - 1968.

Station	1967						1968					
	I	II	III	IV	V	VI	I	II	III	IV	V	VI
Spring	20.7	18.3	19.3	19.5	19.5	17.6	21.7	19.3	19.2	19.4	17.8	18.3
Summer	24.0	21.5	21.0	21.3	19.6	19.4	29.1	26.8	27.1	22.7	21.5	19.2
Fall	22.4	23.2	22.8	21.7	19.5	—	20.5	24.4	24.1	21.5	21.3	21.0
Winter	14.6	16.1	18.1	18.6	19.4	18.6	14.7	16.4	17.8	20.4	22.0	21.5
<b>For Two Years 1967 - 1968.</b>												
Spring	21.2	18.8	19.2	19.4	18.6	18.0						
Summer	26.6	24.2	24.1	22.0	20.6	19.3						
Fall	21.4	23.8	23.4	21.6	20.4	21.0						
Winter	14.6	16.2	18.0	19.5	20.7	20.1						

As penaeid shrimp are benthonic, bottom temperature is important for their spawning. It is evident from Table 9 that intense spawning occurred within the temperature range of 17 to 29 C. In spring, summer and fall, all six genera appear to breed in waters up to 54 m (temp 18.8 to 24.2 C) and in winter to shift their spawning area to deeper waters where the temperature remained above 19 C. From the present data, penaeids seem to spawn throughout the year, but they move to deeper waters as the season advances from spring to winter. This does not, however, mean that one species spawns all the time. Presence of larvae in plankton is a good indication of spawning activity even in temperate waters as has been shown for the European oyster (Korringa 1957).

#### *Abundance in relation depth*

*Station I* (10 m). The trends in abundance and seasonal distribution of the larvae are depicted in Fig. 3.

Larvae, mostly of four genera, started appearing in fair numbers in May and were present until November. The maximum number taken in one haul was 192 (September 1968, day). Four per cent and 6.3% of all the larvae caught occurred at this station in 1967 and 1968, respectively. This was a unimodal trend of abundance, larvae being caught between May and November in good numbers. Bottom temperature rose from 13.3-15.5C to 21.7-23.1C in April, and dropped in the October-November period from 20.8-23.2 to less than 17 C. These periods of rising and falling temperatures produced more numbers of

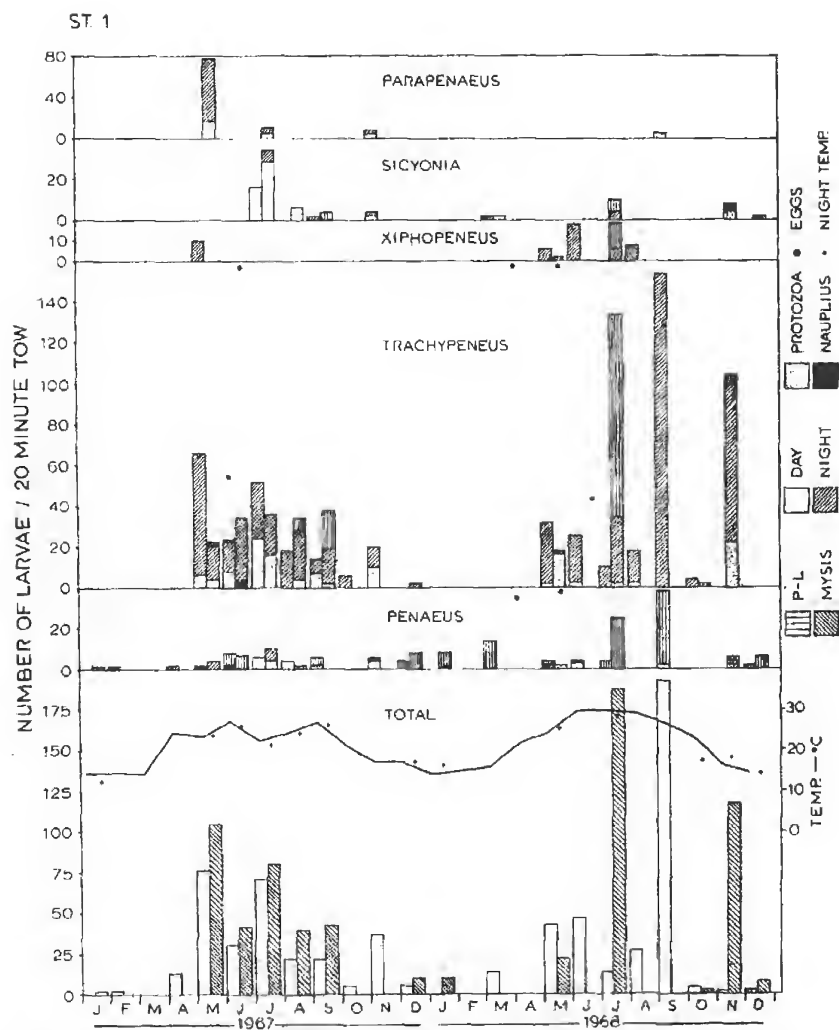


Figure 3. Seasonal abundance, stage and generic composition of penaeid larvae at Station 1 during 1966 to 1968.

larvae. Peaks of abundance were in May to September and in November, i.e., spring-summer and fall peaks. In general, more larvae were caught at night.

*Trachypeneus* was the dominant genus, the number of larvae ranging from 2 to 153 per haul. The spawning season started by April and lasted through November. Spring-summer and fall peaks were evident. Eggs were taken in April (275) and May (40,340) of 1968, and in June (283) 1967; nauplii in June;

protozoae in all months except October; mysids in all months; and postlarvae in July, August, September and November.

Second in the order of abundance was *Penaeus*, the number of larvae varying from 1 to 38 per haul. The breeding season started in April and continued until November. Eggs, probably of white shrimp, were taken in April (35) and May (450) of 1968. Before May only postlarvae of brown shrimp were obtained. White shrimp postlarvae were caught from May to November, but in December only brown shrimp postlarvae occurred. Protozoal and mysis stages first appeared in May. Nauplii occurred only in June. On the basis of the stages of larvae, spawning occurred from April to November.

*Sicyonia* ranked third in numbers, the maximum number of larvae caught being 34 per haul. Though all the four stages were taken in good numbers, protozoae were dominant in July and August 1968. The spawning activity appeared to last from March through November.

*Xiphopenaeus* occurred mostly as mysids and only in five months. The maximum number caught was 20 per haul. Spawning occurred from May to August.

*Parapenaeus* is known to be a deep water genus (Cf. Williams 1965). Fair numbers of larvae were taken in May 1967 (78 per haul). Protozoal and mysis stages were observed at this time, and in July and November also a few of these two stages were caught.

To summarize the trends, spawning of all the species of shrimp appears to begin in April, with rising bottom temperatures and continue through summer and fall. Decreasing temperature in November seems to induce spawning again. This is chiefly a unimodal trend, because spawning continues, once it starts, without a break within the season. *Trachypenaeus* spp. were dominant and *Penaeus* spp. next in abundance. *Sicyonia* is fairly common at these depths, and the occurrence of *Parapenaeus* is considered unusual.

*Station II* (18 m). The greatest numbers of larvae were obtained at this station. The peaks were much pronounced (Fig. 4). The proportion of larvae as percentage of all larvae captured, amounted to 37.8 for 1967 and 42.3 for 1968. Larvae of five genera started appearing in appreciable numbers (over 100 per haul) in May and continued through November. The maximum number obtained was 2543 per haul in October 1968. Peaks were in June and July 1967, and in May, July and October 1968. Indications of spawning activity were apparent in January, but pronounced spawning occurred from May through November. This again is a unimodal trend of spawning. The temperature range during this period was between 19.4 (Novem-

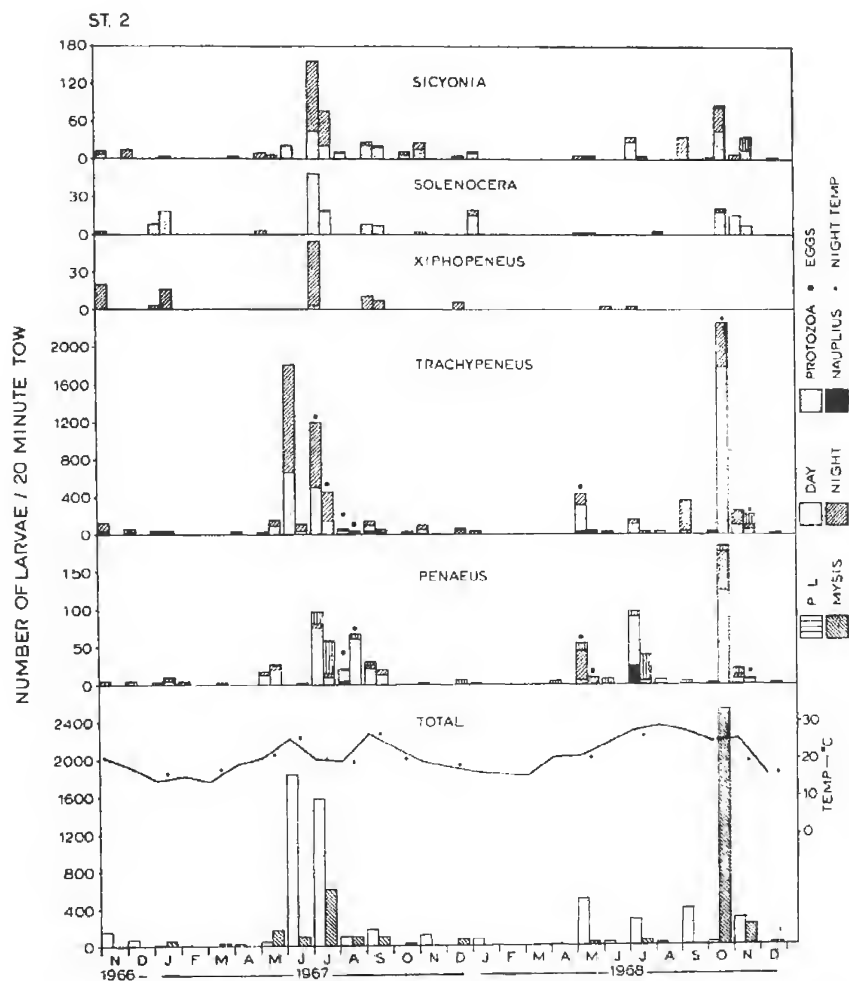


Figure 4. Seasonal abundance, stage and generic composition of penaeid larvae at Station 2 during 1966 to 1968.

ber 1968) and 27.7 C (July 1968). A few early larvae were taken in January when the temperatures were 16.1 and 16.9 C in 1967 and 1968 respectively.

As at the previous station, *Trachypeneus* predominated, maximum number of larvae taken being 2252 per haul (October 1968). Eggs were obtained in July (240) and August (278) of 1967, and in May (1652), October (90), and November (20) of 1968. Nauplii were taken in September 1967 and May 1968. Protozoae occurred in all months; mysids predominated in summer

and postlarvae appeared in November (Fig. 4). Spawning appeared to have occurred from May through November, and the fall peak was higher than the summer peak.

*Penaeus* ranked next in abundance, maximum number of larvae taken being 184 per haul, a higher number than caught at St. I. Eggs were taken in August (52) of 1967 and in May (51) and November (10) of 1968. Nauplii occurred in July 1968 and in August 1967. Protozoae appeared from January to November, and all three stages were caught in varying proportions during the summer and fall months. *Penaeus* species appeared to breed from January to November, with peak activity in summer and fall, the fall peak being higher. Postlarvae of brown shrimp were common in winter, of brown, pink and white shrimp in summer, and again brown and white shrimp in fall.

The next in importance was the genus *Sicyonia*, with a maximum larval production of 155 per haul. Protozoae started appearing in plankton by March and mysids were found throughout. Postlarvae appeared in November. Species of this genus appeared to breed throughout the year with pronounced activity in summer and fall (July and October) at 18 m station.

*Xiphopenaeus* appeared in 7 months and only in the mysis stage. Summer (July) and late fall (November) were peak breeding months. Maximum number of larvae taken was 53 per haul.

*Solenocera* was the new element taken at this depth. A maximum of 48 larvae per haul was taken. Protozoae occurred in all the months, especially July, September, October and November. Spawning season appeared to last from January to November with peaks in summer and late fall.

*Parapenaeus* occurred only twice, in December 1966 and July 1967. All the larvae were protozoae.

From the foregoing it is seen that breeding starts earlier than May, even in January at 18 m. *Penaeus* occurs in greater abundance, and *Solenocera* starts appearing regularly. Minimum temperature at which spawning occurs is 16.1 C, especially for *Solenocera*.

*Station III* (36 m). Fairly large numbers of larvae were taken in these waters, the largest number being 1456 per haul (August 1968). Of the total larvae taken during the 2 years 21.2% and 27.1% were collected at this station in 1967 and 1968 respectively. The bottom temperature range was 16.4 C (March 1968) to 29 C (August 1968). Spawning activity of one species or the other was evident throughout the year, with peaks in July, August, November and December. Intense activity started much later than it did at St. I and II. Heightened spawning in December and January was the interesting feature. The trends in larval abundance are illustrated in Fig. 5.

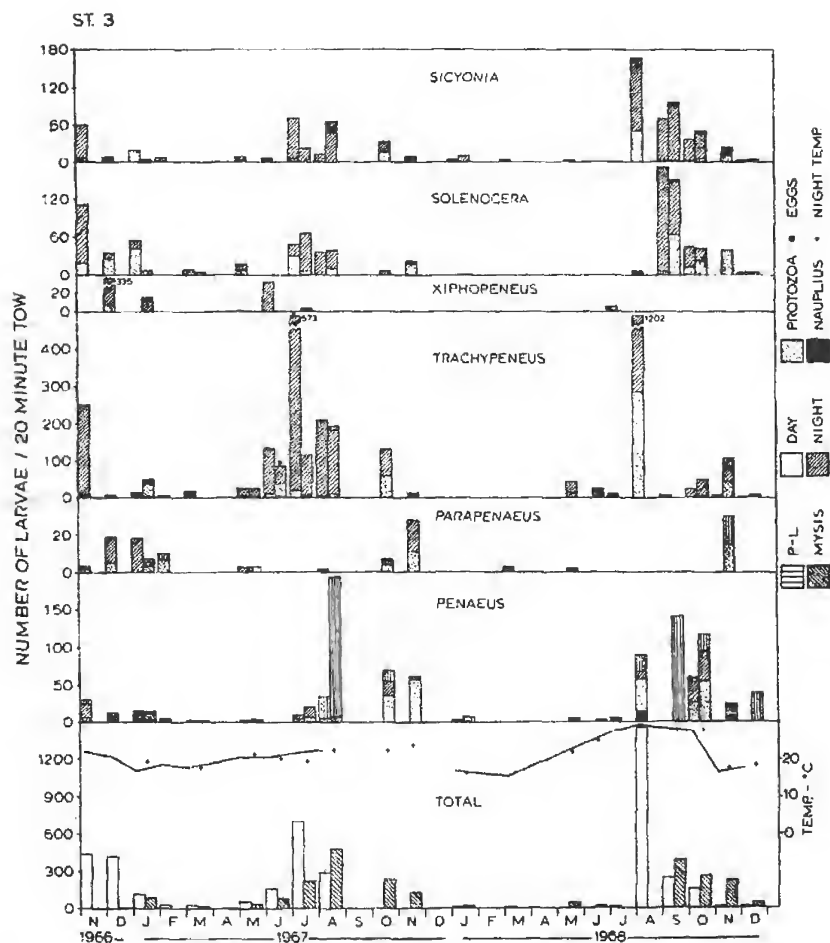


Figure 5. Seasonal abundance, stage and generic composition of penaeid larvae at Station 3 during 1966 to 1968.

*Trachypeneus* was still the dominant genus, with a maximum density of 1202 larvae per haul (August 1968). Eggs were obtained in June (72) and July (10) of 1967 and May (105) 1968. Protozoae, as well as mysids, occurred in every month, mysids being particularly abundant in summer and fall. It appeared that the species of this genus had summer and fall peaks in spawning activity, a bimodal trend, with a less intense period in between the two seasons.

Next in abundance was *Solenocera*, with an observed maximum density of 172 larvae per haul (September 1968). Pro-



tozoeae and mysids were taken in almost all months. Pronounced spawning occurred in January and in March through December, which amounted to year round spawning with distinct periodicity.

*Sicyonia* ranked third in abundance, with a maximum of 166 larvae per haul (August 1968). Protozoeae and mysids occurred throughout the period of study, and postlarvae were abundant in August and November. Peak spawning occurred during July through November. Spawning on a smaller scale in winter was also evident.

*Penaeus* contributed to a fair proportion of larvae, with a maximum of 141 larvae per haul. Spawning started in May and continued through December. In January minor spawning activity was apparent. Protozoeae and mysids occurred during summer, fall and winter. A bimodal pattern of breeding intensity was obvious, with peaks in July-August and October-December. Brown shrimp postlarvae were taken from January to March 1967, and in January and June through December 1968. White shrimp postlarvae were abundant in August 1967 and September 1968.

*Parapenaeus* was a stable element at this depth. Protozoal and mysis stages were caught in almost all the months. Maximum number of larvae obtained was 30 per haul in November 1968. Two periods of intense spawning were observed, January-February and October-December, which was indicative of fall and winter spawning.

*Xiphopenaeus* occurred sporadically, with a peak in December 1966, when 338 larvae per haul were taken.

To summarize, breeding activity of different species is evident throughout the year. This is due to the occurrence of summer-fall spawners, and fall-winter spawners in these waters. *Parapenaeus*, which is a permanent element at this depth, appears to be mainly a fall and winter spawner.

*Station IV* (54 m). The maximum number of larvae taken at this depth was 496 per haul. The total numbers caught amounted to 13.5 and 9.9 per cent of all the larvae taken in 1967 and 1968, respectively. Year round spawning activity was evident with peaks in summer, fall and winter. Bottom temperatures ranged from 17.2 C in January 1967 to 23.0 C in October 1968. The fluctuations in abundance of larvae of the six genera are depicted in Fig. 6.

The deep water genus, *Solenocera*, was the dominant element, with a maximum of 212 larvae per haul (January 1967). Protozoeae and mysids occurred in all the months, and mysids were particularly abundant during summer. Starting off with

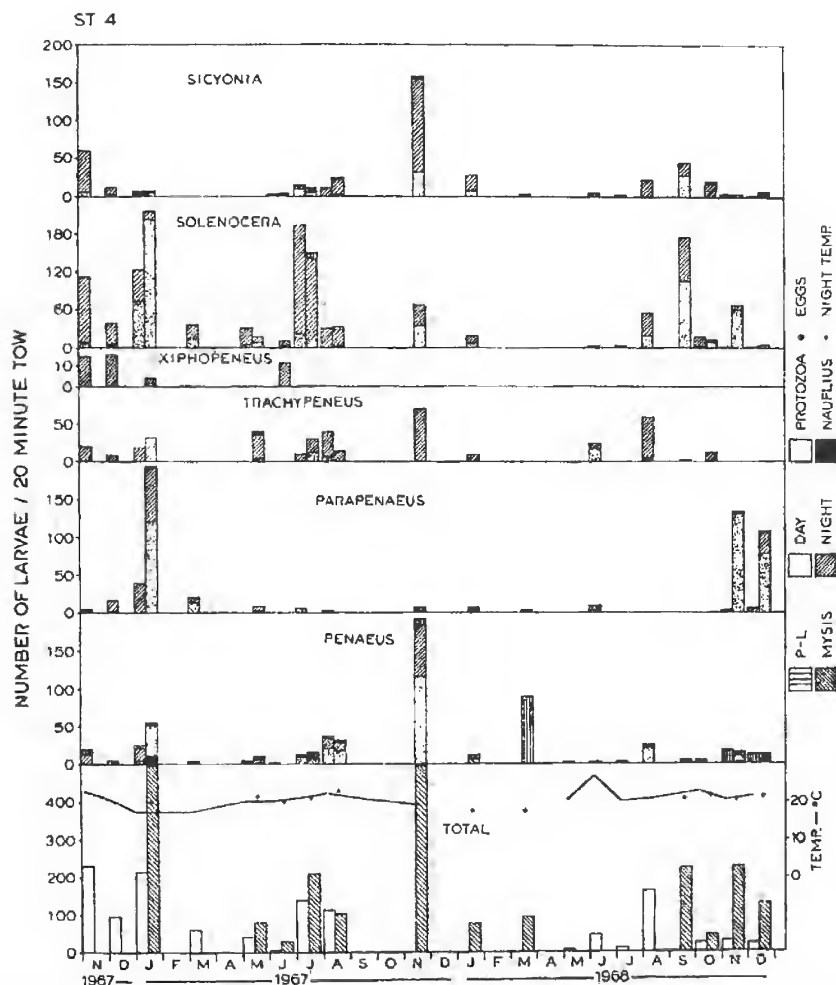


Figure 6. Seasonal abundance, stage and generic composition of penaeid larvae at Station 4 during 1966 to 1968.

a January peak, spawning heightened in summer, continued through September, and again reached a peak in November. Year round activity was evident.

*Parapenaeus* was next in importance, the maximum number caught being 193 larvae per haul (January 1967). Protozoae occurred mainly in January, March, June, November and December. Again there was an indication that species of this genus mainly bred in fall and winter, with minor activity in spring and summer.

*Penaeus* larvae occurred in good numbers, the maximum being 191 per haul (November 1967). Nauplii were taken in January 1967. Spawning started in January, as evidenced by the occurrence of protozoae and mysids, and peak activity was found in August, November and January. Summer, fall and winter spawning was evident. Postlarvae of white shrimp were plentiful in July 1967 and March 1968. Brown shrimp postlarvae appeared in fair numbers in March 1968.

*Sicyonia* larvae were reasonably abundant, the maximum being 159 per haul. Protozoae occurred chiefly from July through December except in October and November. Summer, fall and winter spawning was apparent, with peaks in August, September and November. In these waters, the species of the genus appeared to be mainly fall and winter spawners.

*Trachypeneus* showed a marked decline in numbers of larvae, the maximum caught being only 70 per haul (November 1967). Protozoae were less abundant than mysids. Spring, summer and winter spawning was evident.

*Xiphopeneus* were least abundant, maximum being 16 larvae per haul. Protozoae were scarce and mysids occurred only in 4 months.

It is seen from the foregoing that deep water species, *Solenocera* and *Parapenaeus* spawn intensely at this depth. Year round breeding and a bimodal trend of larval abundance are apparent.

*Station V* (72 m). The maximum caught at this depth was 542 larvae per haul (March 1967). Breeding activity was evident in all the months sampled as can be seen from Fig. 7. Of the total larvae captured 9.4 and 8.4% were obtained in samples from this station. The temperature range on the bottom was 17.8 C in March 1968 to 25.5 C in October 1968. Intense breeding occurred in January, March, July, August, October and November.

*Solenocera* was the dominant genus, with a maximum density of 356 larvae per haul (March 1967). Protozoae were taken in all the months except June, and mysids occurred throughout the year. Spawning was pronounced during winter, spring and fall.

*Parapenaeus* was next in the order of abundance, the maximum number of larvae caught being 177 per haul (March 1967). Protozoae were observed mainly in January, March, May, August, November and December. Mysids occurred in all seasons. Peak numbers were taken in January, March and August, which indicated winter, spring and fall spawning for the species of this genus.

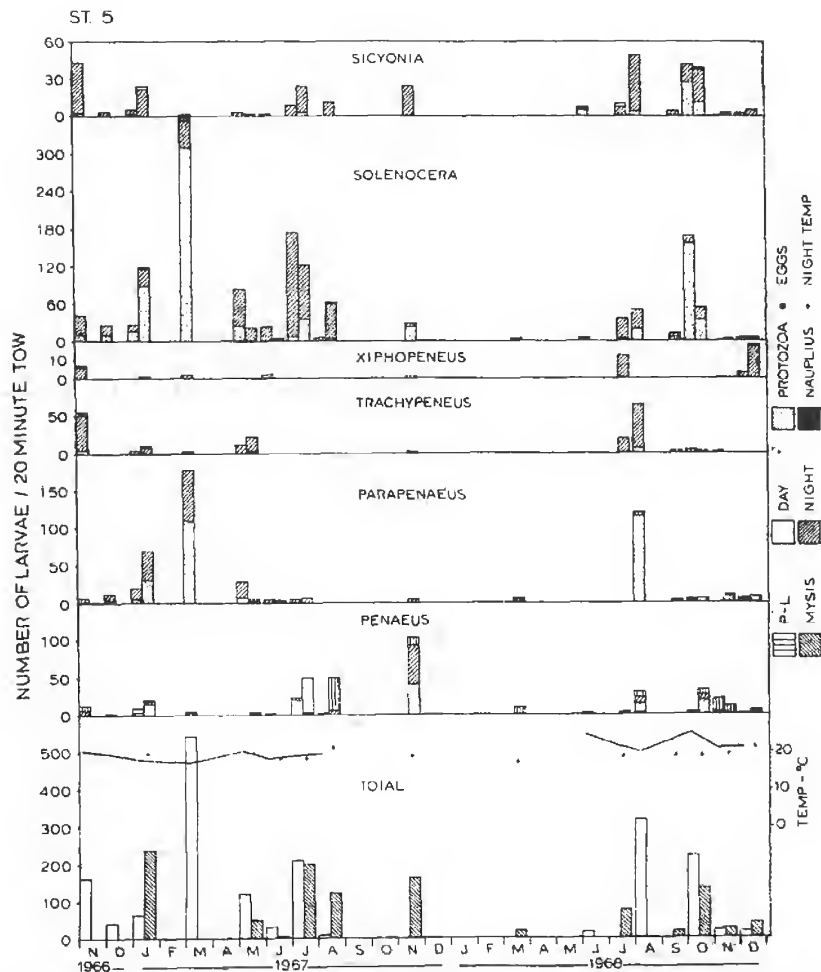


Figure 7. Seasonal abundance, stage and generic composition of penaeid larvae at Station 5 during 1966 to 1968.

*Penaeus* larvae were taken in fair numbers, maximum being 103 per haul (November 1967). Protozoae appeared all through except in March and June when postlarvae were dominant. The same was true for mysids. Postlarvae of brown shrimp occurred in October and November 1968, and of white shrimp in August mainly. Spawning was marked in January, July and August through November.

*Sicyonia* larvae were taken in small numbers, maximum being 52 larvae per haul. Protozoae appeared in May, July-August, and October-November, and mysids were present in all

seasons. Year round spawning with peak activity in January, July, August and October-November was apparent.

*Xiphopeneus* was represented only by mysids in 7 months. The maximum number caught was 18 per haul. The species appeared to breed from August to December at this depth.

*Trachypeneus* larvae were taken sporadically, the maximum being 63 per haul (August 1968). Protozoae were rare compared with mysids.

From the foregoing, the spawning season for all the species appears to be protracted, and breeding occurs even in winter. *Solenocera* species still dominate at this depth.

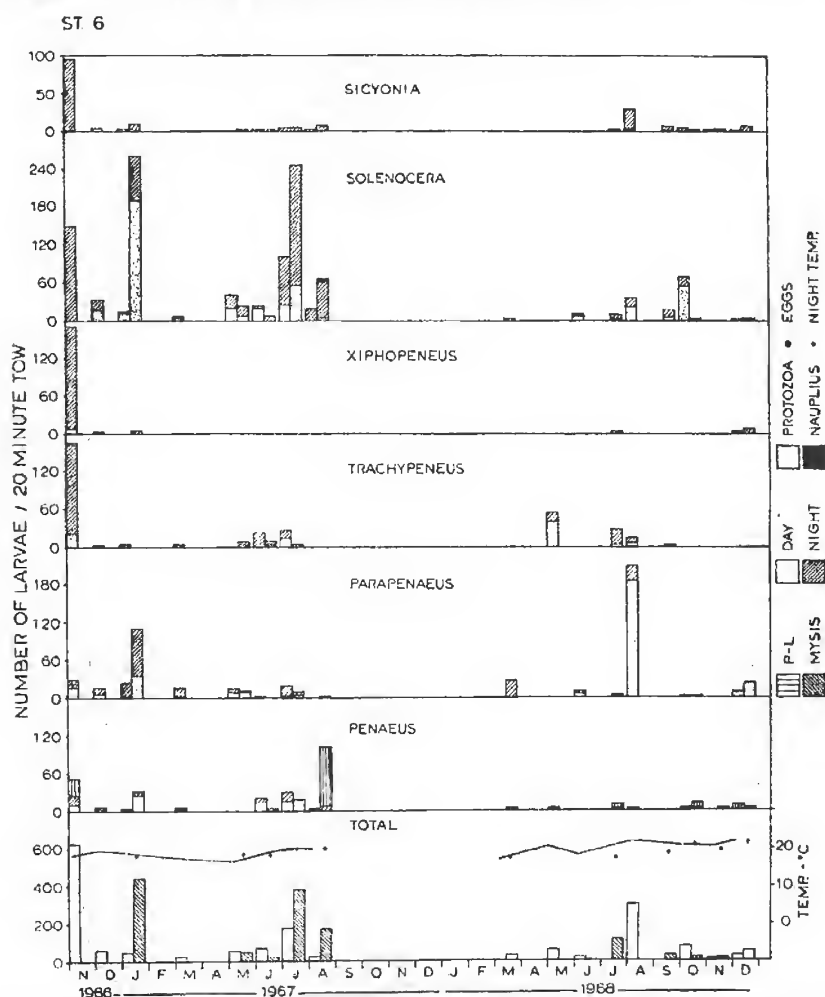


Figure 8. Seasonal abundance, stage and generic composition of penaeid larvae at Station 6 during 1966 to 1968.

*Station VI* (90 m). Data from this station are not complete, but the available information indicated year round breeding activity (Fig. 8). Larval abundance was pronounced in January, July 1967, August 1968 and November 1966. Bottom temperature varied between 17.2 (March 1968) and 21.9 C (August 1967). The maximum number of larvae taken was 642 per haul (November 1966).

*Solenocera* was dominant at this station also, with a maximum density of 260 larvae per haul (January 1967). Protozoae and mysids occurred in all the months. Peak abundance was noticed in January, July, and October-November.

Next in importance was *Parapenaeus*, the maximum number of larvae taken being 208 per haul (August 1968). Protozoae and mysids were taken in all months. Protracted spawning activity, with peaks in January, July-August, and November-December, was evident.

*Trachypenaeus* larvae occurred in fair numbers, with a maximum density of 166 larvae per haul. Protozoae were taken in all months except January and October, and mysids occurred throughout. Peak spawning activity was noticed in June-July and November.

*Xiphopenaeus* was observed sporadically, and the maximum number of larvae collected was 159 per haul. Peak numbers occurred in November 1966.

*Penaeus* larvae occurred in moderate numbers, the maximum taken being 101 per haul (August 1967), and the majority were postlarvae. Protozoae appeared in all months except August, and mysids appeared throughout the year. Postlarval brown shrimp were taken during November and December and white shrimp in August.

*Sicyonia* was the least abundant genus, with a maximum density of 91 larvae per haul (November 1966). Very few protozoae were taken and mysids occurred in all months. The peak spawning seasons appeared to be August and November.

At this station *Solenocera* was still the dominant genus. Protracted spawning activity with winter breeding is observed at this depth.

When the trends in larval abundance at all depths are considered certain patterns become apparent. While spawning activity starts only in spring at 10-m depth, it starts earlier, even in January, at greater depths. Further, a unimodal pattern of abundance is characteristic of 10- and 18-m depths, and a bimodal trend is seen in deeper waters. A gradual replacement of species is obvious as station depth changes. *Trachypenaeus* larvae occur abundantly at 10, 18 and 36 m, and *Solenocera* larvae at 54, 72 and 90 m. *Penaeus* appear in fair numbers at 18 m.

and on either side of this depth larval numbers decrease. *Sicyonia* larvae occur in fair numbers at 10 to 36 m, and the density per haul decreases with increasing depth beyond 36 m. *Parapenaeus* larvae occur rarely in waters shallower than 36 m, but in 54, 72 and 90 m waters larval abundance is second only to *Solenocera*. These trends in the horizontal distribution of the larvae show good relationship with the bathymetric distribution of adults of the species of the six genera.

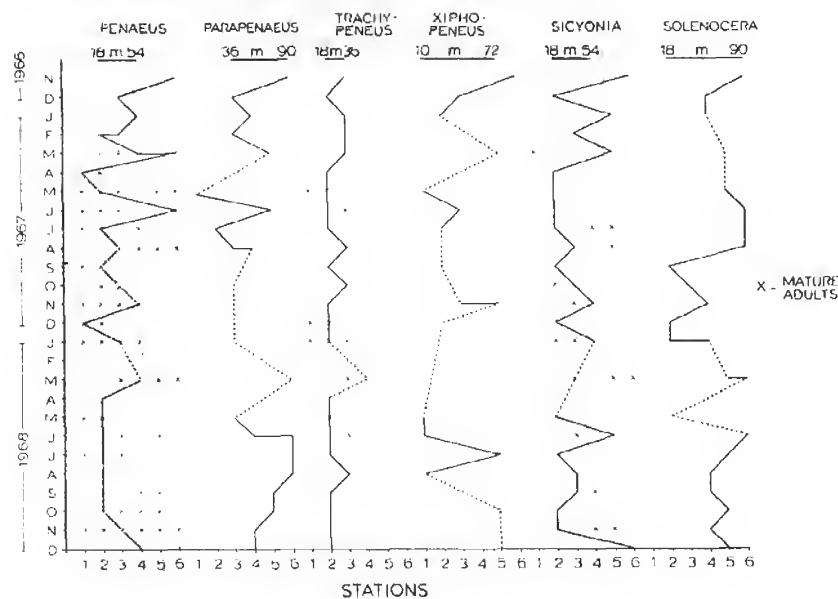


Figure 9. Spawning loci of the six genera in different seasons, within their bathymetric range, as indicated by the larval maxima. (Dotted line indicates no data)

#### Spawning loci of the species

It is to be expected that different species spawn within the range of their bathymetric distribution. Maximal numbers at any specific depth may indicate the center of spawning activity even though larvae can occur at other depths. In Fig. 9 maximal numbers for each genus are plotted in relation to stations, along with the areas where mature adults were captured. This depiction brings out certain trends in the shifting of spawning centers with respect to seasons.

*Penaeus*. In warmer months (April to November) larval maxima occurred at 10 to 54 m, and mostly at 18 m. In early spring and winter months peak numbers were caught at 54 to 90 m. The shifting of breeding center closer to shore in warm months was apparent.

Secondly, adults of white, brown and pink shrimp were taken at all or some of the stations, but larval maxima were observed only at specific depth in a specific month.

The bathymetric distribution of the three species of *Penaeus* is known to be: white from inner littoral to 78 m, brown from inner littoral to 128 m and pink to 109 m (Burkenroad 1939, Eldred *et al.* 1961, Williams 1965, and Saloman, Allen and Costello 1968).

The frequency of capture of the three species during the present investigation is given in Table 10.

**Table 10.** Catch frequency of adults of *Penaeus* species

Station	I	II	III	IV	V	VI
White	8	8	8	1	1	0
Brown	9	13	15	9	9	7
Pink	7	7	1	0	0	0

It is seen from Table 10 that white shrimp concentration was in 10 to 36 m, brown in 10 to 90 m and pink in 10 to 18 m. Probably the summer and fall peaks at 18 m were due to any or all of the three species; those at 36 m due to white or brown shrimp; and those at 72 m and 90 m in winter due to brown shrimp alone. It is also possible that these species may move into deeper waters in colder months to breed there. It is known that white shrimp migrate into deeper waters in winter and a few larvae of pink shrimp have been taken in 180 to 300 m depths off Florida (Eldred *et al.* 1965). Also, each species may have 'preference' for a particular depth as it has been shown in British species of *Leander* (Gurney 1924).

*Parapenaeus.* *Parapenaeus longirostris* is the most abundant species of the genus in the Gulf of Mexico, occurring in depths of 25 to 145 m (Burkenroad 1939, Williams 1965), and *P. americanus* occurs in waters deeper than 200 m (Springer and Bullis 1956). Adults of neither species were caught during the present study. Larval maxima were noticed between 36 m and 90 m stations (Fig. 9). A positive correlation between larval abundance and station depth was found for this species.

*Trachypeneus.* *Trachypeneus similis* was the only species encountered in trawl catches, but *T. constrictus* also occurs in the study area (Burkenroad 1939). The bathymetric range of these



two species is 20 to 37 m for *T. similis* and 5 to 55 m for *T. constrictus* (Burkenroad 1939). *T. similis* were taken at 10 to 36 m.

Larval maxima occurred in 18 to 36 m depths. In summer larval concentrations were noticed mostly at 18 m and during other seasons at 36 m.

*Xiphopeneus*. *Xiphopeneus kroyeri* is the only species of the genus and it occurs mainly in 5 to 36 m (Williams 1965). Larval maxima were observed at 10 to 72 m. Generally, peaks were observed at 10 to 18 m in summer and at 72 m in fall.

*Sicyonia*. *Sicyonia dorsalis*, *S. stimpsoni* and *S. brevirostris* are the three species of the genus in these waters. In trawls both the first and the third species were taken, but *S. dorsalis* was more common. Both the species are known to occur in waters 5 to 85 m deep (Williams, 1965). Larval maxima were mainly restricted to 18 to 54 m, and occasional pulses were noticed at 72 and 90 m (Fig. 9). During summer and fall the concentration of larvae was at 18 to 36 m and in November 1966, and December 1968 it was at 90 m.

*Solenocera*. *Solenocera vioscai*, *S. atlantidis* and *S. necopina* are known to occur off Mississippi, with a bathymetric distribution of 36-72 m, 18-329 m and 5-183 m, respectively (Williams 1965). Generally larval pulses were noticed in depths beyond 54 m during warmer months, and at 18-36 m during cooler months. A positive correlation between abundance and station depth was found for this genus. Species of *Solenocera* are reported to be generally oceanic (Burkenroad 1936).

#### *Larval abundance in relation to occurrence of adults*

Most of the statements on the breeding seasons and spawning localities for shrimps are based on the occurrence of mature adults. Therefore, the relationship between the larval distribution and adult concentrations was examined. Table 11 shows that several times, at different stations, mature adults were taken where larvae were absent. Also, larval maxima and adults did not occur in the same area several times (Fig. 9). Only nauplius and protozoa stages were considered for this correlation study, because their motility is negligible. No significant correlation coefficients for the numbers of larvae and mature adults were found. This indicates that mature adults and larvae need not necessarily occur in the same area, and the locations of adult concentrations do not necessarily indicate precise spawning areas.

**Table 11.** Numbers of mature adult species and larvae (nauplius and protozoa) caught during 1967-1968.

Date	Genus		Penaeus		Trachypeneus		Sicyonia	
	St.	D/N	Larvae	Adults	Larvae	Adults	Larvae	Adults
<b>1967</b>								
Mar. 2	I	D	—	—	—	—	0	1
Mar. 2	II	D	0	1	—	—	—	—
Mar. 21	III	D	0	1	—	—	—	—
Mar. 21	III	N	0	42	—	—	—	—
Mar. 15	VI	D	4	3	—	—	—	—
Apr. 18	II	D	0	1	—	—	—	—
May 18	I	N	0	13	18	2	—	—
May 19	II	D	19	46	1	3	—	—
May 21	VI	N	0	21	—	—	—	—
May 25	III	N	0	9	—	—	—	—
May 25	V	N	1	23	—	—	—	—
June 5	I	N	0	46	—	—	—	—
June 5	II	N	0	12	—	—	—	—
June 22	III	N	0	14	40	14	—	—
June 27	VI	N	3	29	—	—	—	—
July 6	I	N	0	77	—	—	—	—
July 6	II	N	8	45	—	—	—	—
July 25	IV	N	8	10	—	—	6	72
July 12	V	N	—	—	—	—	13	26
Aug. 9	V	D	—	69	—	—	—	—
Aug. 30	IV	N	19	101	—	—	—	—
Aug. 29	III	D	4	5	—	—	—	—
Aug. 8	V	N	—	—	—	—	0	44
Aug. 9	VI	D	0	12	—	—	—	—
Sept. 7	I	N	0	67	—	—	—	—
Sept. 7	II	N	14	92	—	—	—	—
Oct. 27	II	N	6	33	—	—	0	4
Oct. 27	III	N	34	115	—	—	—	—
Nov. 9	I	D	4	51	—	—	—	—
Nov. 14	II	D	2	7	—	—	—	—
Nov. 14	II	N	59	103	—	—	5	1
Nov. 14	IV	N	115	3	—	—	32	7
Dec. 13	I	D	0	53	0	13	—	—
Dec. 5	I	N	0	24	—	—	—	—
Dec. 5	II	N	0	33	2	110	0	3
<b>1968</b>								
Jan. 15	I	N	1	22	0	13	—	—
Jan. 15	II	D	0	31	0	16	0	10
Jan. 17	III	D	0	45	0	2	—	—
Jan. 17	III	N	0	86	—	—	0	5
Jan. 18	IV	N	7	1	—	—	—	—
Mar. 26	III	D	0	9	0	3	0	1
Mar. 26	IV	N	0	1	—	—	0	5
Mar. 27	V	N	0	2	—	—	0	15
Mar. 27	VI	N	0	36	—	—	—	—
May 28	II	N	10	62	10	18	3	5
May 29	I	N	1	22	—	—	—	—
June 19	V	D	0	5	—	—	—	—
June 18	III	N	0	26	10	1	0	2
July 31	I	N	0	85	—	—	—	—

## POSTLARVAL ABUNDANCE IN RELATION TO LARVAL OCCURRENCE

Although larval stages of the three species of *Penaeus* cannot be distinguished from one another, an idea of spawning activity of a particular species might be obtained if postlarval abundance is studied. For this discussion only the postlarvae of white and brown shrimp are considered because of their general availability. Average numbers of larvae and postlarvae per haul (for all stations combined) are plotted in Fig. 10.

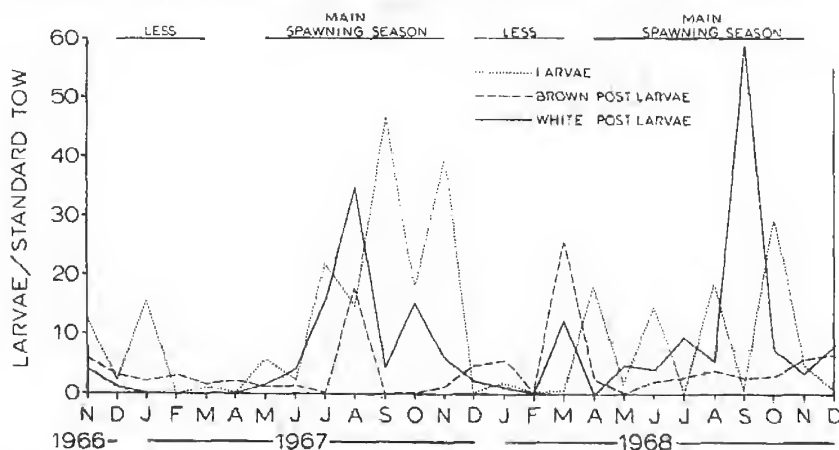


Figure 10. Seasonal abundance of the postlarvae of *Penaeus fluviatilis* and *P. aztecus* in relation to the larval abundance in 10 to 90 m during 1966 to 1968.

The figure shows that the main spawning season for *Penaeus* lasted from April or May to November, with less intense spawning during January to March. During the main spawning season every spawning success was followed by a dip during next month (Fig. 10). Each postlarval peak, either of brown or white shrimp, coincided with dips in larval occurrence. In other words, postlarvae were abundant following each larval peak, which is to be expected because it takes about 10 to 12 days for the nauplii to become postlarvae in summer (Johnson and Fielding 1956). Larval and postlarval peaks were observed in the pattern shown in Table 12.

From the data presented it appears that brown shrimp spawned more intensely in January, March and October, and white shrimp in April, June and August. This does not, however, imply that the two species spawned in succession. Larval peaks of white were observed in shallow waters, and those of brown shrimp in deeper waters. Further, mature adults of *P. fluviatilis* were more frequently caught at 10 and 18 m, while

Table 12. Comparison of larval and white and brown postlarval peaks

Larval peaks		Postlarval peaks	
		<i>White</i>	<i>Brown</i>
1967	January		February
	March		April
	May	June	
	July	August	August
	September	October	
	November		December
			January
1968	January	March	March
	April	May	
	June	July	
	August	September	
	October		November
			December

those of *P. aztecus* were taken at 10 to 90 m during warm months and at 36 to 90 m during winter months. *P. duorarum* was found mostly at 10 to 18 m. Temple and Fischer (1967) arrived at the same conclusion concerning the spawning areas of the three species.

#### VERTICAL DISTRIBUTION

Penaeid eggs are demersal (Pearson 1939, Dobkin 1961, and Subrahmanyam 1965a). Thus, if there is no spring or vernal mixing of waters the early stages may be expected to be found closer to the bottom, and older stages towards surface. The only available information on the vertical distribution of penaeid larvae has been given by Temple and Fischer (1965).

The data on the depth distribution of protozoal, mysis and postlarval stages are illustrated in Fig. 11. Only data for those months in which a complete series of plankton samples were obtained from all the six stations are used for this discussion. Larvae of all the species are treated together.

It is clear that all stages were mixed in various proportions in samples from the three depths at each station. Protozoae were more abundant during peak breeding months.

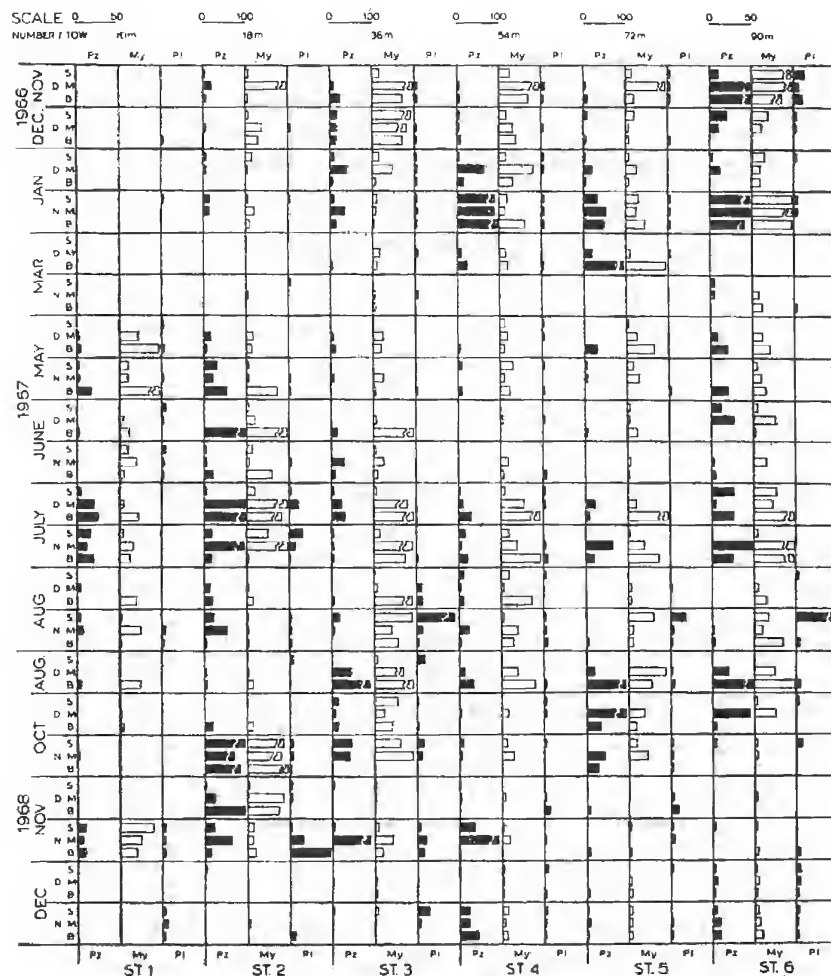


Figure 11. Vertical distribution and diurnal variations of protozoa, mysis and postlarvae at different stations during 1966 to 1968.

Pz : Protozoa (Stipled bars)  
 My : Mysis (Open bars)  
 Pl : Postlarvae (Shaded bars)  
 D : Day  
 N : Night  
 S : Surface  
 M : Midwater  
 B : Bottom

Though the mid-depths of the six stations are not absolutely comparable, protozoal and mysis stages showed a general tendency to aggregate at middle levels.

No statistical correlations between different larval stages, and depth, salinity and temperature were found.

#### *Protozoecal stage*

Protozoecae appeared by May at 10 m and declined by November. In deeper waters they occurred in most months. From December to March they were taken in deeper waters and increasing numbers were taken with increase in depth.

Vertically, in winter months, more protozoecae congregated at the surface and mid-water at 18 to 36 m. They were more evenly distributed in deeper waters during the day. At night there was a general tendency for larvae to move upward and to be more abundant in surface layers, than in mid-water.

In spring the highest concentration was in the bottom during day and night except at 54 and 90 m, in which depths they were often found in equal abundance at the surface and bottom.

In summer months again they were concentrated on the bottom during the day, and mid-water and bottom at nights in all depths.

In fall, the majority were taken in mid-and bottom levels during day, and surface and mid-levels at night.

#### *Mysis stage*

Mysis stages were relatively more abundant than other stages. They appeared in inshore waters by May and became scarce by December. They were taken at all depths in all seasons.

In general, mysids showed a tendency to congregate in mid-layers. In winter they were taken more at the surface and mid-water during the day, and mid-water and bottom at night, except at 36 m where they occurred at the surface. On many occasions they were abundant at surface even during the day.

In spring months during the day they were abundant near the bottom except at 36 and 54 m, where they occurred more often in mid-waters. At night they were near the bottom at 10 m, and in mid-layers in other depths.

In summer, they were more abundant at bottom at all stations during the day. At nights they rose to mid-waters and even to the surface at 54 and 72 m.

In fall, except at 10 m they were more abundant in mid-water during day. They were well dispersed at 54 and 72 m depth, and occurred either at the surface, midwater or bottom at other depths.

### *Postlarval stage*

Postlarvae were taken in small numbers in all depths in all seasons. In general, they occurred more at Stations I to III in winter months. They were more randomly distributed in vertical depths at each station than the other two stages. Occasionally they were taken in greater numbers in surface plankton as in November 1967 (St. VI, day), July 1967 (St. II, night), August 1967 (St. III & VI, night); in midwaters as in July 1967 (St. II, day); or in bottom plankton as in November 1968 (St. II, night). No definite seasonal trends were observed in vertical distribution. Probably their power of motility bestows on them more freedom of movement compared to earlier stages.

From the foregoing it is evident that vertical distribution of protozoal and mysis stages differs with respect to seasons, depths and day and night. At no time was there a definite stratification according to stage, i.e., protozoae at the bottom, mysids in midwater and postlarvae at surface, exclusively. All stages occurred mixed in the meroplankton with varying proportions. In general, depth distributions of protozoal and mysis stages follow similar trends, which emphasizes the fact that these two stages stay together. Unfortunately, not enough nauplii were collected for a discussion of their vertical distribution.

### *Diurnal variations*

The data indicate that night stratification of larvae was not, as a rule, opposite to that during day. On several occasions protozoa and mysis stages were concentrated at the surface during the day, and in bottom plankton at nights. On other occasions both stages were abundant in midwater during both day and night. In general, larvae appeared to be evenly distributed vertically at nights, and to show abundance at a particular depth during day (Fig. 11).

## DISCUSSION

### HYDROGRAPHY

The salinity gradients through depths from 10 to 90 m follow the expected trends with increasing values seaward, and at each station the increasing gradient is from surface to bottom. The fluctuations at each station are complicated by rainfall, land runoff, Mississippi River discharge and currents. How far these seasonal fluctuations affect the breeding seasons is not certain.

Temperature patterns described are typical for any open sea environment. While the surface is subjected to heating by solar radiation, subsurface temperatures are influenced by cur-

rents and advection. The trends of temperature variations shown here agree with those described by Drennan (1968). The minimum and maximum temperatures for any locality are of paramount importance to the breeding activity of marine animals as has been demonstrated by Thorson (1946).

In general, the Gulf of Mexico is unique as far as hydrography is concerned. The existence of semi-permanent rotary circulations in the central Gulf and its effects on northern and eastern waters have been shown by Drummond and Austin (1958), Armstrong and Grady (1967) and Armstrong, Grady and Stevenson (1967). The Mississippi River starts discharging great amounts of fresh cold waters in March of each year (over 10,000 m<sup>3</sup>/sec), and subsides by May or June. Therefore, it is not unusual to find pockets of low salinity waters in March, May and June. It is also evident that the spring discharge influences the temperature profiles at Stations III to V (Fig. 2). The other factors that bring about hydrographical changes in the Gulf of Mexico in general, and the northeastern Gulf in particular, are subtropical underwater currents, the loop current from Yucatan channel through the Florida straits, upwelling in winter, westerly currents from Mobile Bay, and the outflow from Mississippi Sound, and the mixing of different kinds of waters which has been demonstrated by Drennan (1968). Further, surface divergence brings to surface high-salinity, cool waters, and convergence introduces low-salinity, warm waters (Drennan 1968). In view of these factors it is not possible to explain the fluctuations of temperature and salinity off the Mississippi coast in terms of regular patterns.

#### SEASONAL AND HORIZONTAL DISTRIBUTION

Among the several methods that are employed to study the reproductive cycles of marine invertebrates a study of the larval abundance yields fairly reliable information. This method has been adopted by several workers on molluscs and other invertebrates as reviewed by Korringa (1957) and Giese (1959), and on penaeid shrimp by Eldred *et al.* (1965) and Temple and Fischer (1967). The spawning periods and areas have also been delineated by studying the mature adults (Kutkuhn 1962). Both these methods have certain merits and shortcomings. Ripeness of the gonads indicates imminent spawning though unfavorable conditions may set back the process of gamete release. Thorson (1946) has shown that critical temperatures for maturation and spawning are different for many Danish bottom invertebrates. If the temperature is not right, ripe ova may be resorbed as has been shown in oysters by Loosanoff (1969). The spawners may survive the adverse environment and successfully spawn on the return of favorable ambient factors (Loosanoff and Davis 1963). Therefore, conclusions mainly based on the occurrence of mature adults, without taking into



consideration the critical temperature requirements, should be made with caution.

The development of embryos and larvae are also dependent on critical temperature requirements. Cook and Murphy (1965b) have shown that no brown shrimp larvae underwent complete development below 24 C; that naupli did not survive the molt to protozoa I at 18 C and that growth was faster between 27 and 30 C. They obtained the first postlarva after 11 days at 30 C, 12 days at 27 C and 15 days at 24 C. But postlarvae start growing at a temperature between 11 and 18 C, and show maximal growth rate in the temperature range of 17.5 to 25 C (Zein-Eldin and Aldrich 1965, and Zein-Eldin and Griffith 1966). It is not known whether the optimum temperature for growth of larvae and postlarvae is significantly different. Mukhacheva (1959) has shown that eggs of *Eleginus gracilis* (Gadidae) develop only when the temperature is -2.8 to 8C; and eggs of *Crassostrea virginica* do not develop if the water temperature is below 15 C (Loosanoff and Davis 1963). There are certain unproved indications that eggs or larvae of several common marine invertebrates on the Gulf coast may overwinter and suddenly effloresce in the spring. It is possible that spawning may occur at 17 C but the eggs and the larvae may not undergo complete metamorphosis until the temperature rises above 24 C. On the contrary, they may metamorphose at 17 C if the larvae need the same temperature as the postlarvae for maximal growth. However, the occurrence of protozoae, mysids and postlarvae at deep stations even in winter (bottom temperature above 18 C) is interesting. Possibly these larval stages may not grow in winter, but their presence in a water column may indicate previous spawning. With these reservations it is assumed here that spawning occurs in the temperature range of 17 to 29 C. The larvae may take longer time to grow to postlarval stages in the cooler season because the length of pelagic life depends on the ambient temperature (Cf. Thorson 1961). The purpose of the present investigation is to understand the spawning seasons, and does not focus on growth factors of the larvae. The spawning seasons are discussed here with these reservations in mind.

Besides the temperature as a factor, penaeid larvae are subjected to the same ambient factors that affect plankton in general. During the present investigation, as a working hypothesis to interpret seasonal larval pluses at different depths, areas of larval concentration were assumed to represent breeding localities. The movements of the spawners are assumed to be indicated by the occurrence of larval aggregations at different stations. The conclusions based on the larval pulses need not necessarily give an accurate idea of the incidents in the open sea environment in view of the arguments presented hereunder, for and against such a hypothesis.

Some factors that influence the larval distribution are the movements of the organisms themselves, predation, adaptability of the larvae to the environment, transport by currents, and illumination. Thus, nauplii, protozoae and mysids are capable only of feeble movements with the aid of the first antennae (Ewald 1965) and they may not by their own motility travel great distances. Further, penaeid larvae belong to the category of organisms with relatively short pelagic life, (10 to 12 days), and a great stability of occurrence characterizes such larvae (Thorson 1946). Finally, several fish, *Sagitta*, and medusae have been observed to feed on penaeid larvae, and this predation may cause scarcity.

Currents are of great importance for the transport of pelagic animals, and in some cases for survival (Davis 1955). Tidal currents particularly influence organisms in inshore waters less than 15 m deep. Many animals adapt their physiological rhythms to such tidal currents with the results they are transported landward during flood tide as in *Lucifer* (Woodmansee 1966). Thus, tidal currents may transport penaeid larvae from 10 m deep waters into coastal bays. Idyll *et al.* (1962) have shown that currents off the Florida coast are tidal in waters less than 15 m deep, tidal and wind driven at 15 to 33 m depths and density related in deeper waters. Generally spawning grounds are located where strong tides do not exist. Further, it is also possible that shrimp prefer suitable areas for spawning so that larvae will not be exposed to adverse water currents. Johnson (1939) has shown that *Emerita* breed in such favorable areas in relation to currents. Surface currents, essentially wind-produced, may carry the larvae along the flow. On the other hand, subsurface currents are density effected. Heavier organisms such as nauplii, protozoae, mysids, and even eggs are unlikely to be carried away by these currents. These larvae show a tendency to stay in a water column, performing only weak vertical movements. Postlarvae, which can swim forward, are the exception (Ewald 1965). Therefore, sampling at three levels, as has been done in the present study, will compensate for such pelagic transport and may give reliable information on abundance.

Thorson (1946) has shown that a) occurrence of swarms in a particular area to the exclusion of adjacent localities would indicate massive current transport, and b) occurrence of older and younger larvae in different regions indicates current transport. The average fair representation of penaeid larvae in the samples precludes current transport of significant magnitude. Though larval pulses are noticed at certain depths, larvae still occur at other depths. Finally, younger and older stages invariably can be collected from any station and any depth. This appears to be a rule for crustacean larvae in general (Gurney 1924, Pearson 1939, Eldred *et al.* 1965, Temple and Fischer 1965 and 1967). Based on such mixed collections, Gurney con-

cluded that crustacean larvae may not be at the mercy of currents as much as is supposed, and Pearson agreed with him. Though currents influence the distribution of the larvae, larval studies can provide a good idea of spawning activity and locations for penaeid shrimp, in view of the arguments presented here.

Finally, eddies of gyrating currents (non-tidal) are believed to be effective in supporting a self-sustaining population of specific planktonic forms (Sverdrup, Johnson and Flemming 1946, Davis 1955). Where such eddies exist, plankters may not drift too far away from such gyrations but may be circulating in a specific area. That such eddies exist off the Mississippi coast has been shown by Drennan (1968) and Armstrong *et al.* (1967). Therefore, it is possible that penaeid larvae stay in a particular area in the offshore waters for some time after the spawning of the adults. However, postlarvae can swim landward and can make use of tidal currents to gain entry into coastal bays, with the aid of their endogenous tidal activity rhythms (Hughes 1967a).

Both the methods of determining spawning seasons and loci have weak points. While adults can move on their own, subject to circadian and feeding rhythms (Hughes 1967b), larvae are exposed mainly to natural mortality, predation, and current transport. Nevertheless, sampling at three levels and at different depths will yield reliable information on the spawning activity. During the present investigation a good correspondence was found between the seasons of occurrence of mature adults of *Penaeus*, *Trachypeneus* and *Sicyonia* species and of their larvae. Thus, spawning seasons can be delineated based on both factors. However, demarcation of spawning loci based on a single factor may not be accurate. It is likely that a more accurate picture of spawning areas can be based on the occurrence of eggs and larvae if the reservations presented above are borne in mind. Finally, study of the adult or larval concentrations at a specific depth will not yield correct information on the spawning seasons in view of the temperature control of breeding, and of the movements of adults along the increasing temperature gradient.

#### *General*

It has been shown that spawning is pronounced when temperature rises above 17 C. At 10- and 18-m stations, rise of temperature to above 20 C in May, and fall from above 25 C to 20 C in September induce intense spawning activity. As temperature drops in shallow waters shrimps follow a temperature gradient and spawn in deeper waters in winter. Year round breeding is evident if various depths are considered. Orton (1920) states that marine animals are stimulated to breed

either by a specific temperature (physiological constant) or by a rising or falling of temperatures in a particular area. The present findings agree with this rule. Thorson (1946) emphasized that minimum and maximum temperatures are critical for breeding. In the case of shrimps in the Gulf of Mexico the minimum temperature is 17 C and maximum 29 C. Gunter (1957) states, with reference to shallow water species, that all shrimps are spring or summer spawners. Taking the group as a whole, present findings and those of Temple and Fischer (1967) indicate that penaeid shrimps, including deep water species, breed throughout the year in areas where temperature remains within a range of 17 to 29 C. A protracted spawning season, based on larval abundance, has also been reported for *Penaeus duorarum* off the Florida coast (Roessler *et al.* 1967). The European oyster starts spawning when temperature rises above 15 C and continues the activity as long as temperature remains above 15 to 16 C (Orton 1920, Korringa 1957). The environment for the shrimp in the Gulf of Mexico appears to lead to an analogous situation.

These findings point out that penaeid shrimp have protracted spawning seasons. This may be due to a) great vertical distribution of the species, b) different timings of gamete release by younger and older males and females, c) several spawnings of individual females in a season. An extended season implies asynchronous spawning, that is some shrimp are in early stages of maturation, some are getting ready to spawn, some are spawning and others are spent (Giese 1959). Adults caught in the trawls during the present study were in various stages of maturity in any month. Secondly, females of *Penaeus fluviatilis* are known to spawn up to four times a season (Lindner and Cook 1967). Postlarvae migrate into estuaries in two or three waves in summer (Gunter 1950, Lindner and Anderson 1956). After each spawning female gonads rejuvenate and produce more batches of eggs as has been shown for *P. fluviatilis* (King 1948), *P. indicus* (Subrahmanyam 1965b) and four other penaeids (Rao 1968). Lastly, many species have a wide range of distribution (Burkenroad 1934), and younger and older spawners invariably occur mixed in any area. These observations indicate that penaeid shrimp can spawn over a long period of time.

Though the breeding season is protracted, distinct pulses of larvae are observed in spring, summer, fall and winter, depending on the depth of the water column. Mainly there appear to be summer and fall peaks. Periodicity in breeding is a general phenomenon even under stenothermal conditions such as tropical environments, as has been shown for the brackish water fauna of Madras (Panikkar and Aiyar 1939), Great Barrier Reef invertebrates (Stephenson 1934) and *P. indicus* (Subrahmanyam 1963).

It is significant that during spring and summer the spawning center is at the 18-m station. This has survival value for the species because postlarvae have easier access to the estuaries. From 10 to 12 days are required for the nauplius to become a postlarva at 25.6 C (Johnson and Fielding 1956). In colder months this may take longer because temperature controls the length of pelagic larval life (Cf. Thorson 1961). Thus, when the spawning center shifts to deeper waters in colder months the postlarvae still have a chance, if growth is retarded, to enter the coastal bays on the return of warm temperatures. They may overwinter offshore and enter the bays in spring as it has been suggested for brown shrimp along Texas coast (Temple and Fischer 1967).

#### *Abundance in relation to depth*

The data indicate that unimodal spawning occurs in waters up to 18 m deep and bimodal activity in deeper waters. The peaks are observed progressively later in the year as depth increases. In *Penaeus* the summer peak shifts from 10 m in July to 36 and 54 m in August; the fall peak shifts from 10 m during September to 18 and 36 m during October; and to 54 and 72 m in November. A January peak is seen at the 90-m stations. These indicate movements of spawners. Similarly in *Trachypeneus* the fall peak shifts from 10 m during September to 36 and 54 m during October and November. *Sicyonia* shows identical trends. *Parapenaeus* and *Solenocera*, however, do not show such distinct shifts of peaks.

Temple and Fischer (1967) also demonstrated such trends in the shifts of larval maxima. They showed that spawning occurs even in December at 46-m depth, and that the breeding season is more protracted in deeper water compared to the May to October period at 14 m. Eldred *et al.* (1965) have shown that the intense spawning season commenced a month or two later at 10-25-m depths compared to the season in 3-9 m for *Trachypeneus* and *Sicyonia*. Since these authors did not study deeper waters they could not demonstrate year round spawning in depths greater than 36 m, which is a significant point found in the present study. The same authors came to the conclusion that the minimum spawning temperature for *Penaeus duorarum* is 23.9 C, but they later collected larvae at 25-to-36-m depths when the temperature was 19.2 C. It is clear, therefore, that spawning occurs in the temperature range of 17 to 29 C and the spawners move along with the increasing temperature gradient with depth.

The spawning seasons delineated by various authors for different species are in agreement with the present findings. Most of the authors, however, studied a particular depth and the occurrence of mature adults there. When the larval abun-

dance is studied, taking into consideration a wide range of depths, year round spawning activity becomes apparent. Spawning may start early in deeper waters and last longer, while in shallow waters it starts later and ends earlier.

#### *Spawning loci of the species*

The spawning areas of the different species of the six genera show a good correlation to the bathymetric ranges given by Burkenroad (1934) and Williams (1965). The species with a wide bathymetric range breed as close to the shore as possible during warm seasons and offshore during cooler months. It is interesting that *Parapenaeus* and *Solenocera* spawn at 18-to-36-m depths in the cooler season and at 54-to-90-m depths during summer. When shallow water species are spawning in the area of their depth range, species of these two deep water genera have moved out to deeper waters. In the cooler season, when the shallow water species move offshore, the deep water species move into shallower waters.

It has been shown that though the species spawn in their entire range of distribution they prefer certain depths in specific seasons. Eldred *et al.* (1965) were also able to observe such shifts in the spawning loci. They showed that *P. duorarum* spawned intensely either in 3 to 9 m or in 25 to 38 m; *Trachypeneus* in 3 to 9 m; *Sicyonia* species in 3 to 38 m with distinct seasonal pulses at specific depths; and *Parapenaeus* chiefly beyond 25 m. Ingle *et al.* (1959) pointed out that large females offshore may have less rigid temperature requirements for spawning, but it is more likely that penaeids can spawn year round in deep waters because of small scale offshore temperature fluctuations.

Thus, larval maxima indicate spawning loci of the species, and definite seasonal trends in the occurrence of peaks at specific depths argue against effective current transport. Pressure changes at certain depths may also regulate the release of larvae or embryos as has been shown for *Spirorbis borealis* (Knight-Jones and Morgan 1966). Therefore, it is possible that the maximum number of eggs may be liberated by females at favorable depths. The larvae, in view of their power of keeping together (Gurney 1924), may not drift too far away from such area until they become postlarvae. Although the larval pulses shed light on the movements of the spawning population, adults may not be captured during larval peak abundance.

#### *Larval abundance in relation to occurrence of adults*

No correlations were found between adult numbers and larval abundance. This would mean either that the adults moved away from the area of spawning, or that the larvae

were carried to the sampling areas by currents from some other areas. However, the ecological requirements of adults and larvae are not identical, and spent females may have different needs. It is significant that several times adults, but not larvae, were captured in specific areas. *Penaeus plebejus* and *P. esculentus* do not necessarily spawn in their areas of concentration (Racek 1955). It is more likely that adults can move far and wide with the benefit of their activity controlled by a circadian and a 24-hour feeding rhythm (Hughes 1967b), while larvae have feeble motility. Further, adults were not taken at the 10- and 18-m stations where thousands of eggs were collected (Figs. 3 and 4). Thus, here is additional evidence that determination of spawning loci based on the adults does not always yield the correct picture.

#### POSTLARVAL ABUNDANCE IN RELATION TO LARVAL OCCURRENCE

Following every larval peak a postlarval peak, either white shrimp or brown shrimp, is noticed in the open sea. White shrimp postlarvae are abundant in March, May, June, July and September, and intense spawning occurs at 18-m depth during these months. Christmas *et al.* (1966) have shown that white shrimp postlarvae start appearing in Mississippi Sound in May, reach a peak in June, July or August and decline by October. Thus, there is good correlation between the two trends. The Sound postlarvae come from broods in the open sea.

Postlarvae of brown shrimp first appear in the inside waters in February, and reach a peak in April, June and August. The abundance in the open sea bears a positive relationship to that in the Sound. However, fair numbers of postlarvae occur in December and January. Since brown shrimps appear to breed in deep waters during this period, it is likely that these larvae overwinter offshore and move into the estuaries in February or March. Temple and Fischer (1967) came to a similar conclusion in view of the slightly larger size of the postlarvae during the January to April period. Further, postlarvae bury themselves in mud at temperatures lower than 17 C and become active only at higher temperatures (Aldrich *et al.* 1968).

It may be possible to predict the shrimp fishery in Mississippi Sound based on a larval index in the open sea. Following a spawning success, postlarvae can be expected to enter the Sound within three or four weeks. The average annual production of pink shrimp protozoa in South Florida has been estimated to be  $87.0 \times 10^{11}$ ; the survival rate was 74 to 98% per day; 0.05 to 0.14% of the original protozoecal population survived to become postlarvae; and 6% of the postlarvae survived to produce the commercial catch of  $5 \times 10^5$  individuals in



1963 (Roessler *et al.* 1967). Such calculations can be based on the larval numbers obtained by sophisticated sampling. Also, from a long range study it is possible to predict the recruitment seasons for the postlarvae in the estuaries as has been shown by Williams (1969) in North Carolina waters. Because of their fast growth rate, a millimeter or more per day in summer (Viosca 1920, Gunter 1950, and Williams 1955), postlarvae can reach commercial size in three months. Therefore, a larval peak in open sea should be followed by maximal commercial catches in four or five months, allowing a wide margin for the hazards of dispersal, mortality, predation, unfavorable temperature and other ambient factors that affect larvae in the open sea and postlarvae in the coastal bays. It also appears that from the time of hatching about six or seven months are required for the subadults to return to the sea to become mature adults. This surmise is in agreement with the earlier findings of various authors. An uncertain correspondence between postlarval abundance and commercial catches has been shown (Christmas *et al.* 1966). On the other hand, Williams (1969) has shown that no correlation existed between the two factors off North Carolina during a period of 10 years. As the evidence is not conclusive, it will be interesting to examine the relationship between larval, postlarval and commercial catch indices.

#### VERTICAL DISTRIBUTION

No chronological abundance of stages in vertical depths can be demonstrated, and concentrations of protozoal and mysis stages can be expected at any level in any season in any depth. Protozoae and mysids have more or less similar, though not identical, patterns of distribution. Postlarvae seem to be distributed at random in vertical depths in all seasons. Larvae of marine invertebrates in general are known to be positively phototactic. The organisms become negatively phototactic as they grow older (Thorson 1946). It is probable that both protozoal and mysis stages may assemble at levels where optimum light occurs. It is not understood why they do not migrate to surface, as a rule, at night.

Temple and Fischer (1965) state, based on collections from four cruises, that during June, July and September protozoal and mysis stages occur more abundantly near the bottom, while in November they are more evenly distributed vertically. The present, more extensive data indicate that no such definite patterns occur in the summer and early fall months. Even in fall, greater concentrations can be found in bottom layers. Further, during winter both stages were taken in maximal abundance at the surface, even during the day.

Vertical distribution of planktonic animals, including meroplankters, is controlled by several factors, such as direction and speed of movement of species (Szlaeur 1963), hydrostatic pres-



sure (Hardy & Bainbridge 1951, Knight-Jones and Quasim 1955), and salinity, oxygen, dissolved nutrients, viscosity and density (Russell 1927). It has been shown that animals in the upper part of a population respond more to light, and those in bottom layers more to temperature. The depth at which any group occurs reflects isolume movements in the upper part and isotherm movements in the lower part of the population. Also, random movements about an optimal depth result in vertical spread (Moore 1956). Light is believed to be a major factor in distribution (Cushing 1951). Further, four major types of responses in relation to hydrostatic pressure are known to occur in planktonic animals with respect to vertical distribution, namely (1) orientation to gravity alone, (2) orientation to gravity with the subsidiary effect of light, (3) orientation to light alone and (4) no response to pressure changes. Increased pressure induces positive phototaxis, and decreased pressure, passive sinking (Knight-Jones and Morgan 1966). Larvae can also avoid depth changes by endogenous reversals of phototaxis. Responses to pressure changes also depend upon the physiological state of the species (Knight-Jones and Morgan 1966). Temperature changes also influence vertical distribution. Warming and cooling of water may influence heliotropism, altering it from negative geotropism to positive geotropism; and temperature rise may bring about negative phototropism and *vice versa* (Russell 1927).

During the present study only temperature and salinity were considered, and since so many factors are involved in regulating vertical spread of larvae, it is difficult to explain the patterns of vertical seasonal distribution of protozoal, mysis and post-larval stages. However, isothermal conditions during winter and fall combined with less illumination at the surface may explain the wider vertical spread of the stages during these periods, even during the day. In summer the larvae are seen to be more restricted to bottom layers during day and to bottom and midwater at night. Sometimes larvae were absent in the surface waters (Fig. 11), possibly because of more illumination of top layers and negative phototropism induced by temperature rise.

Crustacea, including planktonic larvae, are known to perform diurnal migrations (Russell 1925 and 1928). An excellent review on the subject is given by Bainbridge (1961). The mechanisms for these migrations appear to be active swimming, vertical currents, viscosity of water layers and temperature changes. Several factors such as light, gravity, pressure, temperature and phytoplankton are believed to affect vertical diurnal migrations. The combined effects of light, temperature and pressure changes in a day cycle appear to be the more important (Moore 1955, 1956).

Although a 24-hr study was not made during the present investigation, there are indications that larvae have a tendency to rise toward the surface at night, or that they are evenly distributed in the vertical column. Second and third protozoaeae and mysids have been reported to undertake considerable vertical movements; they may aggregate at a depth or spread out depending on optimum conditions. It has not been demonstrated that, as a rule, planktonic shrimp larvae congregate in the surface layers during night. However, they may be scarce at the surface from midnight to midday, and may rise to surface layers from midday until the following midnight (Roessler *et al.* 1967). Temple and Fischer (1965) claim that such larvae show a distinct ascent to surface at night. However, their data do not lend themselves to such broad postulations. Postlarvae appear to behave more in a classic diurnal rhythm of ascent and descent, though not always. The present data indicate that protozoal and mysis stages do not congregate, as a rule, in surface layers with the advent of night. Random patterns of distributions are more prominent. Since information on the behavior of penaeid larvae is lacking, interpretation of the diurnal patterns of vertical distributions through seasons is not possible.

It is concluded, therefore, that protozoa and mysis stages show random patterns of vertical distribution; show a tendency to be in midwater layers; congregate near the bottom during summer months; show a tendency to rise to the surface in winter months; and show no stratification in a water column in relation to the ontogenic stage. Postlarvae are randomly distributed. Though typical diurnal migrations to surface from bottom and back are not observed, there is a general tendency on the part of the larvae to rise toward surface layers or to become more evenly distributed vertically, in response to decreasing light.

#### SUMMARY AND CONCLUSIONS

1. An investigation was carried out from November 1966 through December 1968, on the relative abundance and seasonal and spatial distribution of penaeid shrimp larvae off the Mississippi coast of the Gulf of Mexico.
2. Six stations were established between 29°N and 30°N latitude, and between 88°12'W and 88°47'W longitude. The depths of the stations were: St. I, 10.7 m; St. II, 18.3 m; St. III, 36.6 m; St. IV, 54.9 m; St. V, 73.1 m and St. VI, 91.5 m.
3. Plankton collections were made with a No. 3 Nylon closing net, that had mesh size of 0.33 mm, length of 2 m and diameter of 50 cm across the mouth. Three simultaneous

tows of 20 min duration were made at surface, midwater and bottom levels at each station. Attempts were made to obtain a complete series of day and night collections every month.

4. Penaeid larvae were separated from the rest of the plankton and identified to stage and genus. They were preserved in 5% buffered formalin (with borax and glycerine). Larvae studied represented six genera, namely *Penaeus*, *Parapenaeus*, *Trachypenaeus*, *Xiphopenaeus*, *Solenocera* and *Sicyonia*.
5. Trends and patterns of salinity and temperature of the area are described and discussed. The fluctuations of these two factors are brought about by Mississippi River discharge, eddy systems and other kinds of water movements and mixing. While bottom temperatures fell to 12 C in the inshore waters in winter they remained uniformly above 16 C in 54 to 90 m throughout the study period. Isothermal conditions existed in winter and fall, while some mixing was evident in spring. In summer, thermal stratification was evident only in 10 to 18 m.
6. Temperature changes were more marked at the 10-m station and less marked at the 72- and 80-m stations. The range of variation was 17.8 C, between 12.3 and 30.1 C, at Station I, and diminished to 9.4 C, between 17.4 and 26.8 C, at Station VI. Surface temperatures fluctuated with a greater range than mid-water and bottom temperatures. The range was 12.2 to 30.4 C, 12.2 to 31.0 C, and 12.5 to 29.5 C at surface, midwater and bottom, respectively, at Station I; and 17.8 to 30.4 C, 17.2 to 28.0 C and 17.2 to 21.9 C respectively at the three levels at Station VI. Bottom temperature varied from 12.5 to 26.1 C in 10-m depth, the range decreasing gradually with increasing station depth. The variation was between 16.7 and 20.0 C in 90-m depth.
7. Salinity fluctuated from 18.5 to 36.6‰ in 10-m depth and the range decreased at deeper stations, the variation being between 26.8 and 38.0‰ at the 90-m station. Surface salinity varied more than mid-water and bottom salinities at all the stations. The ranges for the surface, mid-water and bottom at Station I respectively were 13.1 to 37.1‰, 19.0 to 37.6‰ and 19.9 to 37.6‰, and for the three levels at Station VI were 23.2 to 38.0‰, 23.3 to 38.0‰ and 26.6 to 38.0‰.
8. Determinations of spawning seasons and areas were made by considering the abundance of eggs and of nauplius, protozoal and mysis stages of the species of the six genera.

9. No correlation was found between the occurrence of mature adults of *Penaeus* spp., *Trachypeneus* spp. and *Sicyonia* spp. and of their larvae in a particular area. Adults were taken in some depths where larvae were scarce and *vice versa*.
10. In general, spawning of all species of the six genera seemed to occur within the bottom temperature range of 17 and 29 C. Intense spawning was associated with rising temperatures in spring and falling temperatures in late fall or winter. As long as the temperature remained above 17 C spawning activity prevailed. A unimodal pattern of spawning was observed at 10- and 18-m stations; and a bimodal pattern at 36-, 54-, 72- and 90-m stations.
11. The spawning season of penaeids studied was protracted with distinct pulses in spring, summer, fall and winter. During spring larval concentrations were observed at the 18-m station, during summer at 18-to-36-m stations, during fall at 18-to-54-m stations and during winter at 54-to 90-m stations. This indicates that species breed close to shore during warmer months, and move away from inshore waters as temperature starts falling.
12. Species of *Penaeus*, *Trachypeneus*, *Xiphopeneus* and *Sicyonia* spawned mainly from April to November, and even in winter in waters deeper than 54 m. Species of *Parapenaeus* and *Solenocera* bred intensely during fall, winter and spring. While shallow water species spawned in all depths of their bathymetric range during warmer months, deep water species like *Parapenaeus* and *Solenocera* spawned in deeper waters. During the cooler season shallow water species moved offshore and deep water species moved into waters less than 54 m deep. Then there appeared to be some overlapping between the inshore and offshore species as far as the breeding areas were concerned.
13. *Penaeus* larvae occurred in all depths, *Trachypeneus* mainly between 10 and 36 m, *Solenocera* beyond 18 m, *Sicyonia* in all depths, and *Parapenaeus* mainly beyond 18 m. The larval distribution showed a relationship to the bathymetric distribution of the adults.
14. When maximal numbers of larvae were considered, definite inshore and offshore movements within the bathymetric range of species, were obvious. *Penaeus* spp. spawned in all depths, mainly at 18 m in summer, 36 m in fall and 72 to 90 m in winter. These larval maxima could belong to white and pink shrimp in shallow waters, and to brown shrimp in deep waters. *Trachypeneus* spp. mainly spawned at 18 to 36 m, *Xiphopeneus* at 10 to 72 m, *Parapenaeus* at

56 to 90 m, *Sicyonia* at 18 to 54 m, and *Solenocera* at 18 to 54 m. Larval maxima, thus, give some indication of spawning loci of species.

15. The relationship between spawning success and postlarval abundance of white and brown shrimp was examined. During the main spawning season increase and decrease in larval numbers in alternate months was noticed. For every corresponding valley in the larval abundance curve there was a postlarval peak, either of *Penaeus fluviatilis* or *P. aztecus*. The patterns of occurrence of postlarvae of these two species in the open sea agreed with those observed in Mississippi Sound during a study made previously in the area. Though it is not possible to distinguish the larvae of the three species of *Penaeus*, some understanding of spawning activity of each species can be derived from postlarval abundance.
16. The vertical distribution of protozoal, mysis and postlarval stages of all the genera has been studied. Protozoal and mysis stages showed similar patterns in their vertical spread. During the spring and summer months they were more restricted to sub-surface layers during day, and occurred in upper layers at night. In winter months they were found in large numbers in surface layers even during day. In general, they showed a tendency to aggregate in mid-water layers and sometimes at the surface. Postlarvae showed random patterns of vertical distribution. Temperature, light and pressure appeared to be the main factors controlling depth distribution.
17. A stratification of larvae in vertical profile in relation to ontogenic chronology was not found. Even when there was no vertical mixing of water protozoae occurred in surface layers, and postlarvae could be found in good numbers near bottom. Eggs were found mainly either near the bottom or in mid-waters.
18. The classic pattern of diel migrations was not shown either by protozoal or mysis stages. In general, they showed a tendency to ascend to upper layers during night or to spread out evenly. Even during daylight hours they could be found at surface, and at night near the bottom. Postlarval distribution in the vertical column was random with respect to the diel cycle.

#### ACKNOWLEDGMENTS

It is my pleasure to express my gratitude to Dr. Gordon Gunter, Director of the Gulf Coast Research Laboratory, who made it possible for me to come to Mississippi to make this investigation. I also wish to express my appreciation to sev-

eral members of the Gulf Coast Research Laboratory staff for extending various courtesies during my stay and investigation at the Laboratory.

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